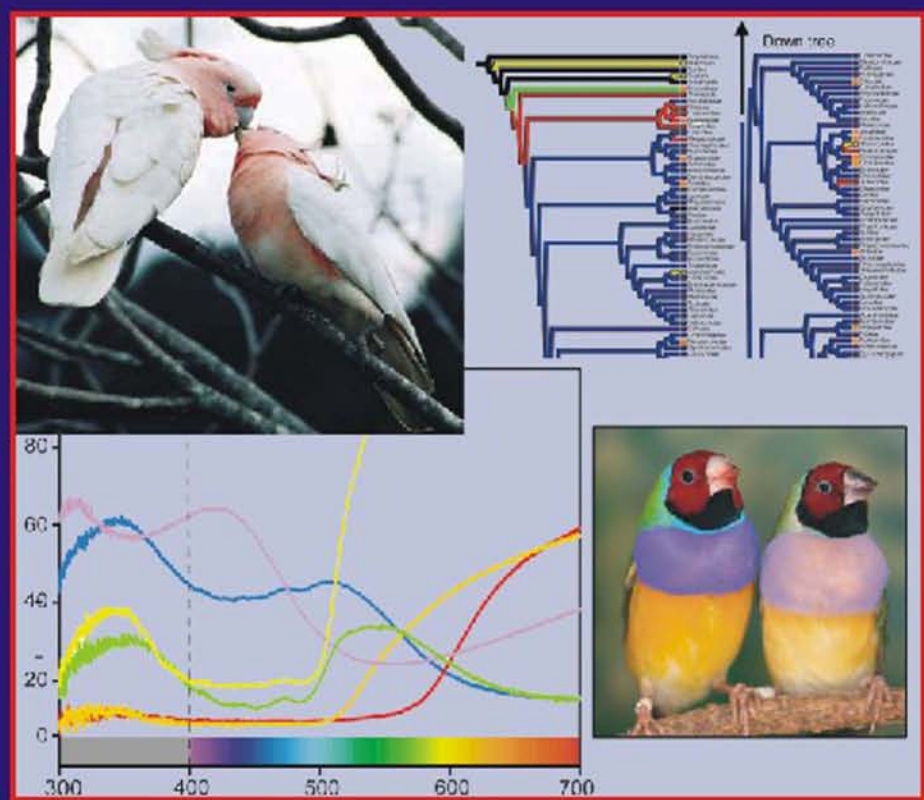


Reproductive Biology and Phylogeny of Birds

Sexual selection ■ Behavior ■ Conservation
Embryology ■ Genetics

Volume edited by
Barrie G.M. Jamieson



Volume 6B of Series:
Reproductive Biology and Phylogeny

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BARRIE G.M. JAMIESON

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Sexual Selection ■ Behavior ■ Conservation
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Reproductive Biology and Phylogeny of Birds

Part B

Sexual Selection ■ Behavior ■ Conservation
Embryology ■ Genetics

Volume edited by
BARRIE G.M. JAMIESON

*School of Integrative Biology
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Preface to the Series

This series was founded by the present series editor, Barrie Jamieson, in consultation with Science Publishers, in 2001 and bears the title '*Reproductive Biology and Phylogeny*', followed in each volume with the name of the taxonomic group which is the subject of the volume. Each publication has one or more invited volume editors (sometimes the series editor) and a large number of authors of international repute. The level of the taxonomic group which is the subject of each volume varies according, largely, to the amount of information available on the group, the advice of proposed volume editors, and the interest expressed by the zoological community in the proposed work. The order of publication of taxonomic groups reflects these concerns, and the availability of authors for the various chapters, and it is not proposed to proceed serially through the animal kingdom in a presumed "ladder of life" sequence. A second aspect of the series is coverage of the phylogeny and classification of the group, as a necessary framework for an understanding of reproductive biology. Evidence for relationships from molecular studies is an important aspect of the chapters on phylogeny and classification. Other chapters may or may not have phylogenetic themes, according to the interests of the authors.

It is not claimed that a single volume can, in fact, cover the entire gamut of reproductive topics for a given group but it is believed that the series gives an unsurpassed coverage of reproduction and provides a general text rather than being a mere collection of research papers on the subject. Coverage in different volumes varies in terms of topics, though it is clear that the standard of the contributions by the authors is uniformly high. The stress varies from group to group; for instance, modes of external fertilization or vocalization, important in one group, might be inapplicable in another.

The first six volumes on Urodela, edited by Professor David Sever, Anura, edited by myself, Chondrichthyes, edited by Professor William Hamlett, Annelida, edited by Professors Greg Rouse and Fredrik Pleijel, Gymnophiona, edited by Professor Jean-Marie Exbrayat, and Birds (first volume), edited by myself, reflected the above exacting criteria and the interests of certain research teams. The sixth volume, in two parts, has resulted from my interest in the natural history of birds, which was stimulated in childhood by Gilbert

White's incomparable '*Natural History of Selborne*', and my good fortune now in being joined by a most distinguished group of authors who need no introduction to those familiar with avian studies. A further volume in preparation is on Cetacea (Debra Miller).

My thanks are due to the School of Integrative Biology, University of Queensland, for facilities, and especially to the Executive Dean of the Faculty of Biological and Chemical Sciences, Professor Mick McManus, for his continuing encouragement. I am everlastingly indebted to Sheila Jamieson, who has supported me indirectly in so many ways in this work. I am grateful to the publishers for their friendly support and high standards in producing this series. Sincere thanks must be given to the volume editors and the authors, who have freely contributed their chapters, in very full schedules. The editors and publishers are gratified that the enthusiasm and expertise of these contributors has been reflected by the reception of the series by our readers.



THE UNIVERSITY
OF QUEENSLAND
AUSTRALIA

10 August 2006

Barrie G.M. Jamieson
School of Integrative Biology
University of Queensland

Preface to this Volume

There are almost ten thousand known species of birds of which more than half are songbirds. They are an ideal subject of study as they are one of the few groups of animals for which almost the total number of species is estimated to be known, they have been comprehensively catalogued and illustrated and are readily identified in the field whereas groups such as annelids (Volume 4) require detailed microscopical work for identification. Besides these practical qualifications for study and the biological questions that they pose, they have endeared themselves to humanity not least for their beauty and their song. Volume 6, in two parts, attempts to document most of the important aspects of the reproductive biology of birds and places them, in the first part particularly, in a setting of phylogenetic relationships. Aspects of reproduction that comprise this, the second part of volume 6, are sexual selection of ultraviolet and structural signals; melanins and carotenoids as feather colorants and signals; sexual selection and auditory signaling; odors and chemical signaling; sexual dimorphism; sexual selection, signal selection and the handicap principle; courtship and copulation; sexual conflict and its implications for fitness; intra- and extra-pair paternity; parental care (including cooperative breeding); brood parasitism; applications of reproductive biology to bird conservation and population management; embryogenesis and development; molecular genetics of avian sex determination and gonadal development. Many new illustrations are provided throughout the volume.

The generosity of authors and publishers who have allowed illustrations to be reproduced is most gratefully acknowledged. The kind collaboration of all the authors, who have borne uncomplainingly the requests of an editor overseeing the gestation of this work, has been greatly appreciated. Finally, the courteous and efficient participation of the publishers was indispensable to production of this volume.



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10 August 2006

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Sexual Selection of Ultraviolet and Structural Color Signals

Sarah R. Pryke

1.1 INTRODUCTION

As a class, birds are renowned for their bright, often bizarre and even gaudy plumage coloration. Classically, the diverse and typically sexually dimorphic plumage colors of many birds—and thus the obvious importance of color vision in their biology—has provided much of the stimulus in the study of visual sexual communication. In fact, as the numbers of empirical studies on sexual selection have accelerated over the last decades, avian plumage coloration has been at the forefront.

However, it is only recently that the colorful plumages of birds have been investigated from the avian perspective. Although biologists have long recognized that the perceptual world of their animal subjects may escape our own sensory abilities, for example, while ultrasound, echolocation, and electroreception are recognized as sensory dimensions that we can only appreciate in the most general terms, surprisingly this view did not extend into the visual capabilities of birds. This is despite the long recognition that avian vision is amongst the richest in the animal kingdom (Walls 1942; Meyer 1977; Goldsmith 1990), and that the evolution of colorful plumage displays implies well-developed color discrimination. Yet, just as the invertebrate and fish biologists recognized a few decades ago, avian biologists may also be blind to many important aspects of coloration in birds and their perception of the environment. Perhaps the most striking example is that near-ultraviolet light (wavelengths 320–400 nm) is a normal part of hue perception in the lives of birds (Bennett and Cuthill 1994; Cuthill *et al.* 1999), but is a spectral region to which humans are blind.

So why has the sensory perception of such well-studied and visually orientated animals been overlooked for so long? Technological constraints are in part to blame. The equipment necessary to accurately take objective and

relevant measurements of visual physiology and plumage reflectance has only recently become available (and affordable). In addition, there also appears to have been a lack of cross-disciplinary dialogue between avian physiologists and behavioral ecologists working on the evolution of color in birds. However, the main reason is most likely related to our own color perception: because vision is such a fundamental part of our lives, it is difficult to imagine another vertebrate perceiving the world in a different way. Perhaps work on insects (and to a large extent fish) preceded and far outpaced that on birds (e.g. Daumer 1958; Avery *et al.* 1983) because insects seem different enough that their vision is expected to differ fundamentally from ours.

The first evidence of birds' sensitivity to ultraviolet (UV) light came from behavioral discrimination experiments in the 1970's with Pigeons (*Columba livia*) (Wright 1972) and Hummingbirds (*Colibri serrirostris*) (Huth and Burkhardt 1972). Hummingbirds seemed an appropriate target to investigate because they pollinate flowers, and evidence from insect research showed that UV-reflectant markings on flowers served as nectar-guides for pollinating insects (Goldsmith 1980). Since then, behavioral and electrophysiological experiments have demonstrated UV vision to be the norm among diurnal birds (see Bennett and Cuthill 1994), and UV vision has, by one means or another, been shown in over 35 species representing 8 orders (see Bennett and Cuthill 1994; Bowmaker *et al.* 1997; Hart *et al.* 1998, 1999, 2000; Cuthill *et al.* 1999), with negative evidence for only two nocturnal owl species (Bowmaker and Martin 1978; Koivula *et al.* 1997). In fact, UV vision is widespread, both among vertebrates and invertebrates (Bowmaker 1991; Jacobs 1992; Goldsmith 1994; Tovee 1995), and is even found in some mammals (Jacobs *et al.* 1991; Jacobs and Deegan 1994), so this capacity is far from unusual.

Thus, equipped with new technology and a new outlook, studies of sexual selection have begun to quantitatively and objectively measure color and relate it to aspects of avian behavior and ecology. In fact, the number of sexual selection studies on structural coloration has dramatically increased in the last few years, with the majority of studies focusing on the UV component. Part of our fascination with UV coloration is likely linked to the unknown—the 'hidden dimension'—a perception which we can never fully comprehend. Yet, while the discovery of UV reflectance has led to expectations of an important function for UV in sexual color communication, rigorous empirical studies demonstrating this are still scarce. Is UV/structural reflectance a specially adapted sexual signal or simply a byproduct of feather structure? What is the relative importance of UV versus other colored or sexual traits? What are UV signals signaling? This chapter begins with a brief review of how structural and UV signals are perceived and produced, before examining the current progress and findings of structural and UV signals in sexual selection. In particular, this chapter will hopefully address the large gaps in our knowledge and highlight some of the exciting future challenges in the study of sexually selected bird coloration.

1.2 AVIAN UV COLOR VISION

Before discussing how birds may communicate using UV color signals, it is important to understand, and highlight, how bird vision differs from that of our own visual system. Both color science (e.g. Jacobs 1981; Wyszecki and Stiles 1982) and avian vision (Bennett and Cuthill 1994; Cuthill *et al.* 1999) have been reviewed in detail elsewhere, and therefore I will only briefly outline the areas pertinent to color vision and UV detection.

Color vision is a psychophysical phenomenon that exists only in our minds (see e.g. Wyszecki and Stiles 1982; Thompson *et al.* 1992), with an object's color dependent not only on the relative amounts of different wavelengths of light it reflects, emits or transmits, but also on the sensory properties of the observer. The sensation of color stems from the differential stimulation of several types of photoreceptors in the retina of the eye. Each cone type produces an output (transmitted to the brain), and it is the relative differences in output at a particular point on the retina that underlies the sensation of color. Thus, it follows that species with different receptor sensitivities (e.g. their cones are sensitive to different wavelengths of light), or those comparing the information received from receptors in different ways, will see the color of objects differently.

Avian vision differs from that of humans in three principal ways that are likely to produce major differences in their color perception (see Bennett and Cuthill 1994 for review). First, most birds are able to detect near-UV light, wavelengths shorter than 400 nm (to which humans are blind because of a UV-absorbing lens; Goldsmith 1990; Jacobs 1992). Because of ozone absorption in the upper atmosphere, little natural UV light is available at wavelengths much shorter than 300 nm. Subsequently, compared to the visual range of humans (400-700 nm), birds can perceive a wider spectral range (typically 320-700 nm).

Second, the retinas of birds and humans differ in the number and type of light sensitive cones present. Humans possess only three single cone types, which are maximally sensitive to wavelengths of light in the blue, green and red regions of the human visible spectrum (see Fig. 1.1). In contrast, birds possess six cone classes: four types of single cones, and the two dissimilar double cones, which are also found in fish and turtles (Liebman and Granda 1971; Ohtsuka 1985), but are lacking in humans. While the function of the double cones remains unknown (Hart *et al.* 1998; Wilkie *et al.* 1998), current evidence suggests that they are not used in color vision (Vorobyev *et al.* 1998; Vorobyev and Osorio 1998). The avian single cones span the avian-visible spectrum fairly evenly, although there is some variation between species in the wavelengths of maximum sensitivity of their visual pigments. Most birds, including the Passeriformes (and Budgerigar) have a true UV visual pigment, with a maximum sensitivity around 355-380 nm. In contrast, in the Anseriformes, Ciconiiformes, Columbiformes and Galliformes, the UV-sensitive cone is replaced with a violet-sensitive cone (λ_{max} 400-426 nm). The

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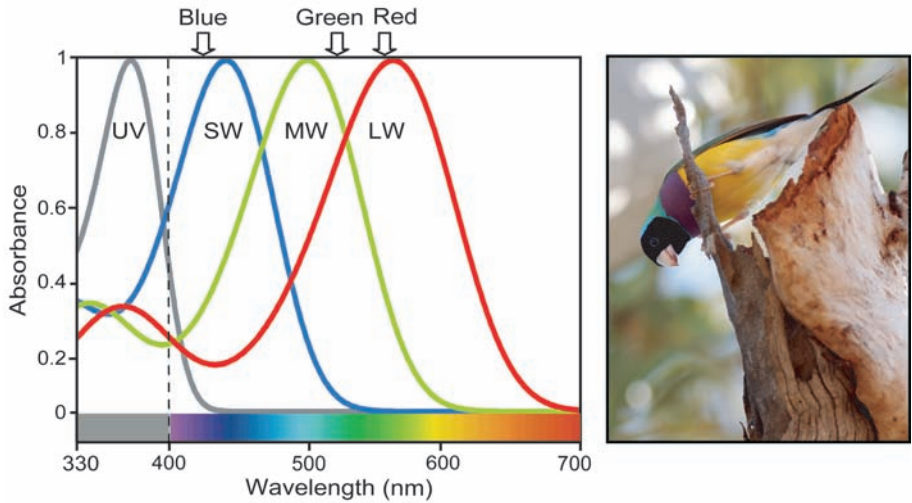


Fig. 1.1 Normalized absorbance of the visual pigments from the four types of single retinal cone cells in the Gouldian finch (*Erythrura gouldiae*): UV = ultraviolet, SW = shortwave, MW = medium wave, LW = longwave. Curves are the best-fitting visual pigment templates for the average spectra based on microspectrophotometry. For comparison, the wavelengths of maximum spectral sensitivity of the blue, green and red cones of humans are indicated by arrows at the top of the figure. Redrawn and adapted from Hart *et al.* 2000. *Journal of Comparative Physiology, Series A* 186: 681-674, Fig. 2A. Photo showing male black-headed Gouldian finch inspecting a nest hollow. Photo: Sarah R. Pryke.

reasons for this dichotomy between bird families are unknown at present (Bowmaker *et al.* 1997; Yokoyama *et al.* 1998; Yokoyama *et al.* 2000), but importantly, both the UV and violet sensitive cones allow birds to see in the UV. The three other single cone pigments are more similar in their spectral sensitivity, but not without some variation (Hart *et al.* 1998): short-wave ($\lambda_{\max}$ 430-463 nm), medium-wave ($\lambda_{\max}$ 497-510 nm) and long-wave ($\lambda_{\max}$ 543-571 nm) sensitive visual pigments.

Lastly, in birds, each of the four single cone photoreceptors contains a different type of oil droplet through which light must pass before reaching the visual pigment (for a review see Hart 2001). In all but one of the cone types, the oil droplets contain carotenoid pigments (i.e. short-wavelength absorbing pigments) that act as cut-off filters of the incoming light. This narrows the absorption peak, shifting it to longer wavelengths before the light reaches the light sensitive part of the cones, and thereby reducing overlap between adjacent spectral types (Bowmaker 1991, Bowmaker *et al.* 1997; Maier 1994b).

Consequently, birds differ from humans, not only in their sensitivity to the UV spectrum which increases the range of wavelengths over which they can see, but also in their superior ability to detect and discriminate spectral differences, perhaps even within the human visible spectrum. Together, this

produces a change in color perception that cannot be translated into human experience—birds don't see what we see, and vice versa.

1.3 UV/STRUCTURAL COLOR PRODUCTION

Structural coloration is widespread in nature, found in a number of vertebrates, invertebrates and even leaves (Auber 1957; Fox 1976; Dyck 1976). In birds, structurally-based plumage includes the white, ultraviolet, blue, violet, turquoise and iridescent colored patches of feathers (Auber 1957; Dyck 1974). In contrast to pigment-based, and typically longer-wave coloration (e.g. carotenoids and melanins; see Chapter 2), structural-based coloration has received little attention from behavioral ecologists, at least until very recently, when researchers became aware that many structural colors contain a major UV component. In fact, most studies of structural coloration are re-badged as more fashionable 'UV signals', even though the majority of structurally-based studies actually describe a peak reflectance in the visible, not the UV, portion of the spectrum. While there are obvious overlaps, for example blue structural feathers typically contain extensive UV hues, even the avian UV role models, such as Blue tits (*Cyanistes (=Parus) caeruleus*; Andersson *et al.* 1998; Hunt *et al.* 1998), Bluethroats (*Luscinia svecica*; Andersson and Amundsen 1997; Johnsen *et al.* 1998), and Eastern bluebirds (*Sialia sialis*; Siefferman and Hill 2003; Siefferman and Hill 2005a; Siefferman and Hill 2005b) exhibit a peak reflectance in the human-visible range (but see the UV/blue reflectance of Gouldian finches in Fig. 1.2). Indeed, the occurrence of primarily UV

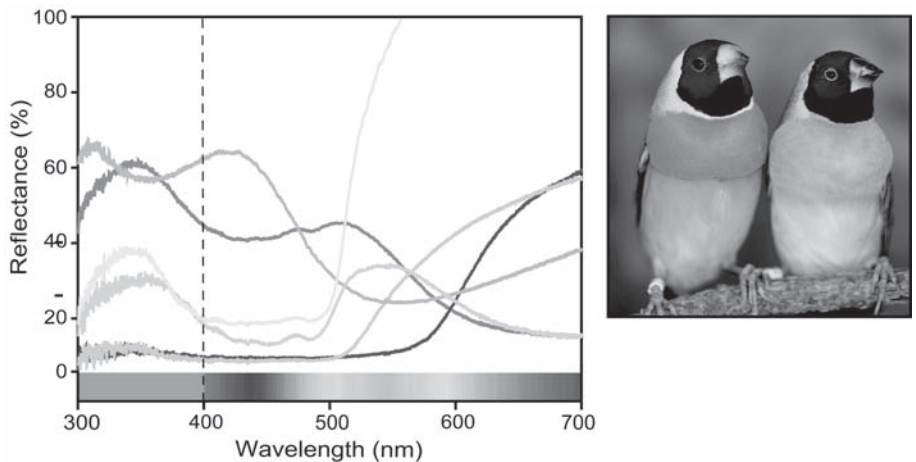


Fig. 1.2 The relative amount of reflectance (i.e. reflectance spectra) of the human visible blue, violet, green, yellow, orange and red colored patches of male Gouldian finches (average of $n = 139$), showing the long wavelength colors of yellow and red pigmentation, and the shorter wavelengths of the blue, violet and green colored patches. Note the strong contribution of UV to the human visible violet and particularly blue colors. Original figure. Photo of red-headed Gouldian finch male (left) and female (right), Photo: Sarah R. Pryke.

reflectance (i.e. main reflectance below 400 nm) is very rare, and well documented in only the *Chalopsitta* cockatoos (Burkhardt and Finger 1991) and *Myiophonus* thrushes (Andersson 1996). Thus, despite the confused and interchangeable jargon used in recent literature, a number of structural colors do not reflect, primarily or otherwise, in the UV. Nevertheless, since structural coloration often contains a UV component, for the context of this chapter I will not strictly differentiate between the signals, referring to them as UV/structural or structural (i.e. without a UV component) as required.

Structural plumage is broadly distributed among birds, and appears to have arisen independently numerous times within the phylogenetic history of Aves (Dyck 1976, 1978; Finger *et al.* 1992; Finger 1995; Andersson 1996). The colors of structural plumage result from small changes in the feather structure that alters their light reflective properties. No exclusively blue-green or UV-colored pigments are known in birds (an exception is found in Touracos (Musophagidae); Moreau 1958), but structural colors in combination with yellow carotenoid or brown melanin pigments commonly produce bright green or darker olive greens, respectively.

Structural-based colors are produced via three different mechanisms, characteristically categorized by their resulting color: (1) iridescent, (2) non-iridescent, including most UV, blue, violet and green colors, and (3) white. Although the discussion below describes how structural coloration is produced in bird plumages, this does not exclude other avian body parts, such as the skin, beaks, legs and feet, in which structural and UV/structural colors may also be created (reviewed in Prum and Torres 2003).

1.3.1 Iridescent Plumage

The first class includes classically iridescent coloration, which are colors that change hue or color with the angle of incidence or observation. Such coloration is created by constructive (or destructive) interference of light waves scattered from melanin granules found within the feather barbules (filaments branching from the feather barbs) (Dyck 1976, 1987; Fox 1976). The simplest mechanism, thin-layer interference, results when incident light is reflected from, and refracted within, the highly refractive keratin layer coating the granular melanin layer of the feather (Fig. 1.3). Alternatively, several layers of keratin may be stacked, along with a number of air vacuoles and melanin granules, in a three-dimensional lattice to produce multi-layered, constructive reflections. Regardless, both mechanisms create an intense and shimmery color when viewed at certain angles; increasing the angle of incidence will cause the color to change to blue or yellow-green, and with greater changes in angle, the color will become black (i.e. reflected light is out of phase). To further intensify these colors, many black birds coat the melanin layer with a thin layer of wax to produce a shinier iridescent effect. The iridescent red, green, blue, and violet colors of Peacocks (Durrer 1965), and the UV/iridescent colors of many Hummingbirds (Trochilidae; Bleiweiss 1994) and European starlings (*Sturnus vulgaris*; Cuthill *et al.* 1999) are produced in this manner.

1.3.2 Non-iridescent Plumage

The second and most common class is non-iridescent structural coloration, which is produced through light scattering structures inside the barbs of feathers (filaments branching from the feather shaft). Barbs contain a specialized spongy medullary layer, which is composed of a heterogeneous matrix of keratin rods and air vacuoles of varying shapes and sizes surrounding a basal layer of melanin granules (Dyck 1971; Fox 1976). The exact physical mechanism of color production by feather barbs is debated (Dyck 1971; Fox 1976; Finger 1995; Andersson 1996, 1999; Prum *et al.* 1999; 2003), but most recent studies suggest that light waves are coherently scattered from the multiple surfaces of the air-keratin matrix (Fig. 1.3). Essentially, the keratin rods and air spaces cause short wavelengths of light (i.e. UV, blue, violet and green) to be coherently reflected (Prum *et al.* 1999; Prum and Torres 2003), while the longer wavelengths (e.g. yellow and red) are absorbed by the basal melanin layer (which also eliminates backscattering from the tissues below). Small changes in the size or arrangement of these elements can cause substantial variation in the resulting reflected color, both among and within species (Dyck 1971; Andersson 1999; Prum *et al.* 1999, 2003; Shawkey *et al.* 2003), and even between the sexes of the same species (Shawkey *et al.* 2005). This mechanism generates most UV, blue and violet structural colors in birds, such as those of the Blue whistling thrush (*Myiophonus caeruleus*) (Prum *et al.* 2003), Eastern bluebirds (Shawkey *et al.* 2003; Shawkey *et al.* 2005) and Gouldian finches (*Erythrura gouldiae*) (Prum *et al.* 1999). Some birds also use this mechanism coupled with multilayer interference to produce predominately UV plumage coloration, which appears black to humans (Finger *et al.* 1992). By placing a thin carotenoid, or more rarely a melanin, layer above this arrangement, violet and blue wavelengths are absorbed and green is the only wavelength scattered, producing the green plumage common to a number of bird species.

1.3.3 White Plumage

Lastly, white is also a structural component which is produced from unspecialized, unpigmented keratin feather barbs (Prum *et al.* 1999). Unlike non-iridescent structural feathers, white feathers contain no melanin, but instead possess many large air cavities, which in conjunction with a number of other large particles, such as molecules of fat, protein, keratin or crystals (Fox 1976; Nassau 1983), reflect all visible wavelengths of light (i.e. incoherent scattering) producing white coloration (Fig. 1.3). Although white is among the most commonly produced color, with many birds typically displaying at least one white patch of plumage, it has received little attention, both as a color itself as well as in the context of structural coloration (see below).

1.3.4 UV-reflecting Pigmented Plumage

Although structurally-based UV reflectance typically produces a peak reflectance in the shorter wavelengths of the spectrum (i.e. UV, blues, greens),

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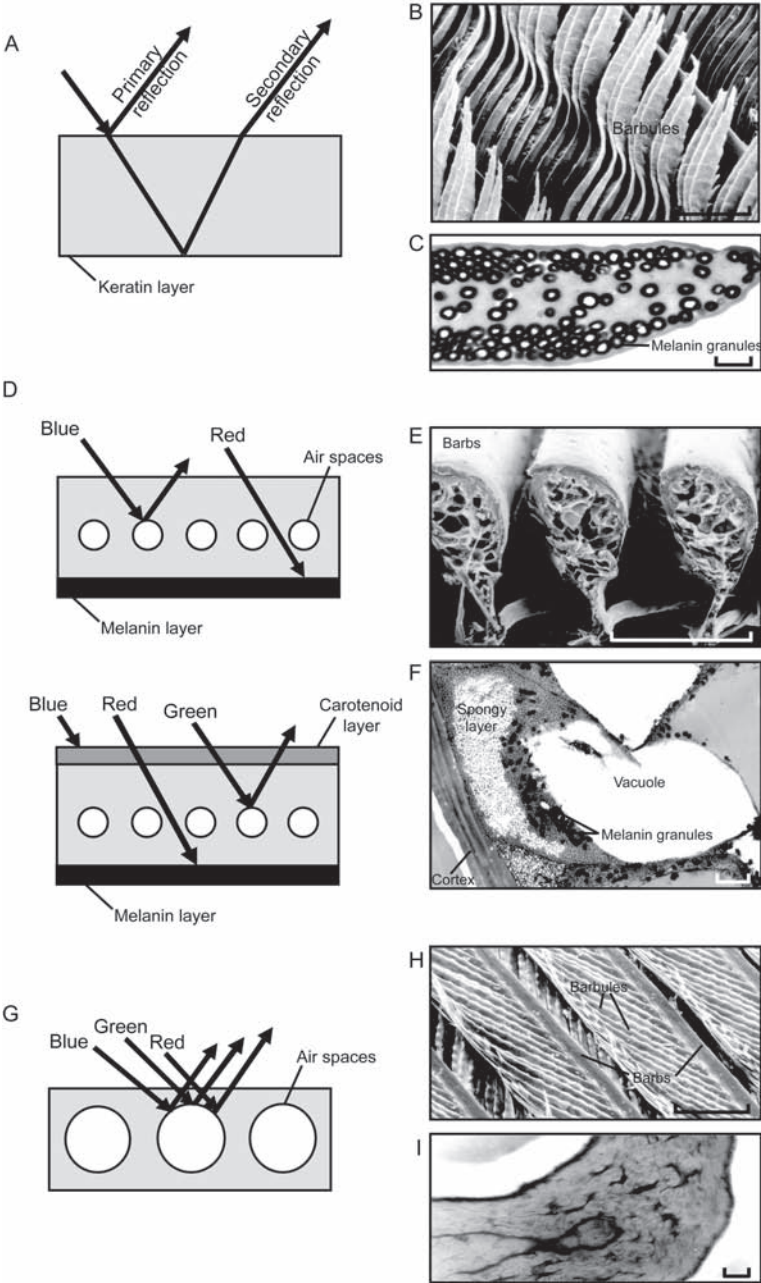


Fig. 1.3 A. Diagrammatic representation of thin layer interference, typical of many iridescent structural colors. When white light is incident on the highly refractive keratin layer, it will produce a primary reflection (with a phase shift) off the top and

UV reflectance is not completely restricted to structural coloration (Eaton and Lanyon 2003; Bleiweiss 2005; Shawkey and Hill 2005). In addition to many green color displays, resulting from a combination of structural and pigmented feathers, spectral measurements have shown that a number of primarily pigment-based plumages also possess reflectance curves with a secondary peak in the UV. For example, an UV component has been reported in the brown-black melanin-based plumage of Pied flycatchers (Siitari and Huhta 2002), and appears relatively common in the yellow to red colors of carotenoid-based plumages, such as those of American goldfinches (Shawkey and Hill 2005), Tanagers (Bleiweiss 2005) and Gouldian finches (see Fig. 1.2). This finding also highlights the fact that the distinction between human visible colors (e.g. reds) and UV colors is not as neat as it may seem. Birds which reflect strongly in the red portion of the spectrum, such as Scarlet ibises and which look bright red to us, also reflect in the UV and therefore probably look a sort of ultra-purple to each other. At present, it is unknown how this UV peak is created. A few recent studies propose that in some carotenoid-based plumages, such as those of tanagers, the secondary UV peak is controlled largely by the carotenoids themselves (Bleiweiss 2005). Conversely, other studies suggest that carotenoids create UV reflectance by absorbing light from another reflective substance, such as the structural white tissue underlying the yellow carotenoid-based feathers of Yellow-breasted chats (*Icteria virens*; Mays *et al.* 2004) and American goldfinches (Shawkey and Hill 2005). However, irrespective of the physical origins of pigment-based UV-reflectance, at present the biological importance and function of secondary UV reflectance, especially in relation to the primary pigment-based color, remains to be shown.

Fig. 1.3 Contd. ...

a secondary reflection (no phase shift) off the lower boundary. When the thickness of the layer and the angle of incidence meet the conditions for a certain wavelength range, the two reflected waves will be in phase with each other and constructively interfere to produce a very intense, colored reflection. Changing the thickness of the layer (by one-half a wavelength) or changing the angle of incidence will result in destructive interference of the two reflected waves, and black will be observed.

B. SEM of a European magpie (*Pica pica*) feather showing barbules. Scale bar = 100 μm . **C.** TEM of a cross-section of a magpie barbule from an iridescent feather. Scale bar = 500 nm. **D.** Light scattering from air spaces and/or keratin rods results in stronger reflection of short wavelengths, and a melanin layer underneath absorbs all other wavelengths, to produce blue coloration. Adding a carotenoid (e.g. yellow) layer, which absorbs the violet and blue wavelengths, produces a green color. **E.** EM cross-section of a blue tail feather from a Blue jay (*Cyanocitta cristata*) showing feather barbs. Scale bar = 100 μm . **F.** TEM of a cross-section of a blue jay tail feather barbs. Scale bar = 2 μm . **G.** Larger air spaces and/or more particles (e.g. molecules of fat, protein, keratin or crystals) scatter all wavelengths and produce white. **H.** SEM of a white European magpie feather. Scale bar = 100 μm . **I.** TEM cross-section of a white magpie barb. Scale bar = 200 nm. Photos: Simon C. Griffith.

1.3.5 Fluorescent Plumage

Finally, a short-wavelength component of plumage coloration which also deserves mention within the context of this chapter is fluorescence. By definition, fluorescence originates from special fluorescent pigments in the feathers (typically green, yellow, orange and red) rather than from the structure itself (Völker 1937; Boles 1991). However, these pigments only fluoresce in the presence of UV light, where short wavelengths of light (UV or blue) are absorbed (by the pigments) and then re-emitted at longer human visible wavelengths (Boles 1991; Pearn *et al.* 2001; Arnold *et al.* 2002). For humans, the fluorescent plumage of birds can only be viewed under a 'black light' (i.e. emits only UV light), where the fluorescent patches literally 'glow'. Fluorescence is thought to be confined to mostly Australian parrot species (Psittacidae), although there are some examples of red porphyrin fluorescence in a few nocturnal species and violet fluorescence in the downy feathers of domestic Turkey chicks (Boles 1991; Sherwin and Devereux 1999). Although originally reported by Völker in 1937, very little work has been done on this unusual property since then, especially in relation to avian signaling (see below).

1.4 MEASURING UV AND STRUCTURAL SEXUAL SIGNALS

Given the profound differences between human and bird vision, it may seem that color studies based on human judgments, when birds are the natural receivers, are likely to be unreliable (Eaton 2005). An example is the well-studied Blue tit, *Cyanistes* (= *Parus*) *caeruleus*, a species with a brilliant blue colored crown, but with reportedly little variation in the color, at least to the human eye (Svensson 1992; Cramp and Perrins 1993). Consequently, earlier studies of sexual selection focused on other aspects of the bird, rather than color itself (Kempnaers *et al.* 1992; Svensson and Nilsson 1996; Kempnaers *et al.* 1997). However, together with the recent advancements of field-portable UV/VIS reflectance spectrometers, it has been demonstrated that the bright blue coloration of the Blue tit is relatively variable and also includes an UV component (Andersson *et al.* 1998; Hunt *et al.* 1998). In particular, the crown, differs substantially between males and females in the UV/blue portion of the spectrum (Andersson *et al.* 1998; Hunt *et al.* 1998, 2001). Compared to females, males have both brighter (i.e. more intense) and more chromatic (i.e. saturated) plumage with reflectance peaking deeper into the UV (Fig. 1.5). This is just a single example to illustrate the potential limitations of using human-based methods in assessing color-based avian traits (see Bennett and Cuthill 1994).

Yet, the opposite trend has probably occurred in more recent years. Although the possibility remains that failing to account for UV reflectance may compromise our ability to understand color signaling in birds (Bennett and Cuthill 1994; Eaton 2005), there is now an added danger of instead over-emphasizing the role of UV signals. In particular, the user-friendliness of

reflectance spectrometers has prompted an explosion of studies simply documenting the presence of UV-reflecting plumage in a number of birds. In many ways, this is to be expected as it is the most obvious difference between bird and human color perception. Undoubtedly, there is UV information in many species' plumage reflectance (e.g. Burkhardt 1989, 1996; Finger 1995; Finger *et al.* 1992; Bennett and Cuthill 1994; Finger and Burkhardt 1994), and many common backgrounds (e.g. leaves, earth and bark) reflect very little in UV (Chittka *et al.* 1994), so UV-reflecting plumage would often be conspicuous. However, just because a bird's plumage reflects in the UV does not mean that this is necessarily an important signal in avian color communication. Because of the UV-content of light backscattered from unpigmented feather keratin (Andersson 1996), UV reflectance from pigmented feathers is likely to be a passive component of coloring primarily in longer wavelengths. Since most UV-reflectance from feathers need not imply a signaling function, this chapter will focus on studies that have implicitly explored the signal function of UV and structural reflectance, rather than the numerous studies merely reporting the presence and/or variation of UV reflectance in avian plumage.

In particular, although UV/structural coloration has likely evolved in many different signaling contexts, such as foraging (Viitala *et al.* 1995; Church *et al.* 1998) and possibly orientation (Coemans *et al.* 1994; Vos Hzn *et al.* 1994; Hunt *et al.* 1999; reviewed in Cuthill *et al.* 2000), this chapter will be limited to purely ornamental color displays, in other words, those used in sexual signaling contexts. Typically, ornamental traits are characterized by high levels of variance across a population, with the most attractive individuals displaying the highest levels of trait expression (Andersson 1994; Andersson and Iwasa 1986). Color-based ornamental traits may vary either in the size of a particular colored patch of plumage or in the qualitative nature of the color itself. For example, the white forehead patch of the male Collared flycatcher (*Ficedula albicollis*) does not vary much in its whiteness, but shows extensive variation in its size. By contrast, the UV/blue crown plumage of the Blue tit varies most significantly in the quality or saturation of the color, with little variation in the size of the colored patch. Typically, individuals with the most intense color or the largest patches are considered to have the highest level of ornamental expression.

1.5 SEXUAL SELECTION AND UV/STRUCTURAL SIGNALS

The first study to show that behavior may be affected by UV-reflecting plumage was Maier (1993) who used behavioral choice tests to demonstrate that Pekin robins (*Leiothrix lutea*) discriminated against roosting with conspecifics when they were viewed in UV-deprived rather than normal UV light conditions. Following this experiment, a number of studies have used similar methods to block UV light in order to specifically look at mate preferences (Maier 1994a; Bennett *et al.* 1996, 1997; Andersson and Amundsen

1997; Hunt *et al.* 1997; Johnsen *et al.* 1998). However, before discussing these experimental studies, it is important to understand the techniques used, since they differ fundamentally from the more traditional methods employed in most color studies (e.g. bleaching, painting and dying pigmented patches of coloration). In fact, one of the major challenges faced by researchers in the field of UV color signaling is to experimentally manipulate only the UV portion of the signal. This is largely because most of the popular products which have been used to successfully mimic the natural variation in other colored plumage, such as marker pens, paints and hair dyes, are designed for the human visible system. Even in structural plumage (without a UV component) few studies have taken this approach and successfully manipulated birds within their natural variation. Nonetheless, for UV/structural signals two main experimental methods have been utilized. The first is similar to that employed by Maier (1993) and uses filters to selectively block UV light (e.g. Bennett *et al.* 1997, 1996; Hunt *et al.* 1997; Maier 1994a), while other studies have applied UV-blocking oils directly onto the plumage (Andersson and Amundsen 1997; Johnsen *et al.* 1998; Sheldon *et al.* 1999). There are a number of pros and cons to both methods. The filter approach is generally used in behavioral mate choice chambers, where different filters are placed between the test and stimulus birds, and therefore this method has the advantage of not directly interfering with the bird. However, even in the more advanced filter experiments where relative brightness (i.e. intensity) is controlled for (e.g. Bennett *et al.* 1996, 1997; Hunt *et al.* 1997), these filters block out not only the UV in the ornamental traits under investigation, but also the whole light environment of the birds (e.g. entire plumage and background). In effect, this is comparable to swapping between colored and neutral glasses, and thus complicates the inference of mate choice, as opposed to species recognition or simply preferences for the most natural illumination and the avoidance of strange-looking birds and environments.

In other experiments, UV-absorbing chemicals, such as those used in commercial sun-blocks, which absorb UV-reflectance but leave human-visible reflectance unaltered, have been used to coat the plumage (Andersson and Amundsen 1997; Johnsen *et al.* 1998; Sheldon *et al.* 1999). Chemical applications are more selective than the filter method, allowing manipulation of specific plumage areas and avoid changing the appearance of the whole bird and its light environment (see Fig. 1.4). However, this approach (at least as done to date) is effectively a supernormal treatment, extending the UV plumage reflectance far beyond the natural variation (i.e. completely removing UV) and thus provides an unnatural cue to mates. Therefore, once again, it is not possible to exclude the possibility that females prefer normal looking males (i.e. with UV) to strange-looking birds (i.e. no UV). Furthermore, this approach provides little information as to whether the natural variation (as opposed to a presence/absence effect) in male UV reflectance is used as a mate choice cue. A better approach is obviously to manipulate color displays within the natural variation, but as mentioned above this has proved difficult

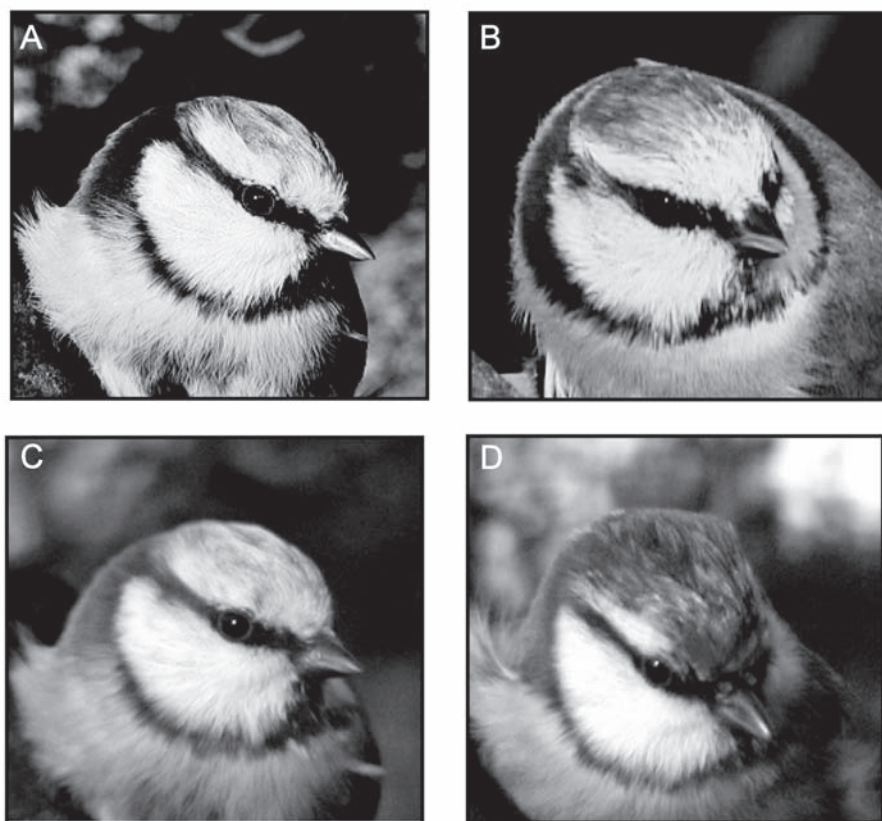


Fig. 1.4 Male Blue tits (*Cyanistes* (= *Parus*) *caeruleus*) have a UV-reflectant crown patch. Photos **A** and **B** show a male Blue tit photographed with a lens that transmits full human visible light, while photos **C** and **D** are taken with a lens that only transmits UV light. To manipulate the UV-reflective crown, sunscreen was applied to the UV/blue crowns (**B** and **D**). Note the large brightness contrast of the crown between untreated (**C**) and UV-blocked birds (**D**) when viewed in UV light alone. Photos: Staffan Andersson.

for colors outside the human visible range. Some treatments, such as blue or black marker pens may be used to alter the brightness (intensity) of UV-reflecting plumages within the normal variation (Ballentine and Hill 2003) but not of the actual spectral color *per se* (i.e. hue or chroma). The limitations of these experimental methods need to be kept in mind when investigating the relative importance of UV/structural cues in sexual selection.

Nevertheless, despite the problems, these methods have produced similar results: UV wavelengths are important to birds and may enhance/reduce the attractiveness of stimulus birds (see Table 1.1). For this discussion, rather than attempting to provide a review of all the studies examining the sexual function of UV/structural coloration (see summary in Table 1.1), I will instead

highlight some of the more well-studied avian systems (see Fig. 1.6), emphasizing our current knowledge (or lack of this) in the study of UV and structural signaling.

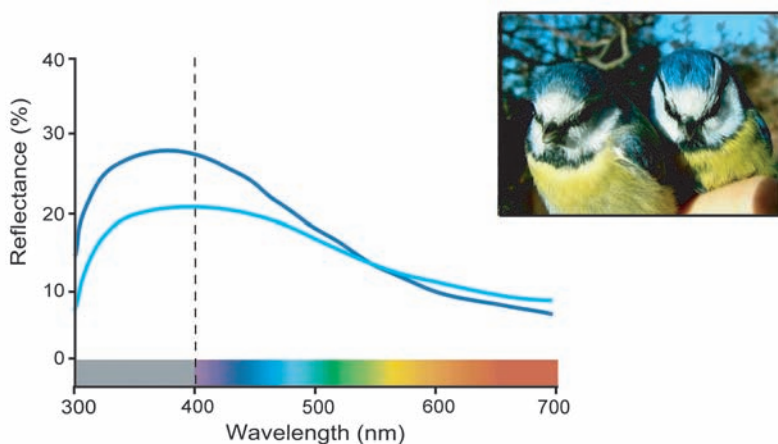


Fig. 1.5 Reflectance spectra for the UV/blue crown plumage of Blue tits, illustrating the sexual dichromatism between males and females. Male Blue tits have both brighter (i.e. more intense) and more chromatic plumage (i.e. saturated) with a larger UV component than females. Photo shows female (left) and male (right) Blue tits. Redrawn from Örnborg *et al.* 2002. *Biological Journal of the Linnean Society* 76: 237-245, Fig. 2.

1.5.1 Avian UV Role Models

1.5.1.1 Zebra finches

Following the earliest experiment on UV-based mate choice, where Bennett *et al.* (1996) showed that female Zebra finches (*Taeniopygia guttata*) directed their behavior towards males under full UV illumination in preference to males behind UV-eliminating filters, Zebra finches have become one of the most commonly cited examples of a bird using UV signaling in mate choice. However, although Zebra finches are something of a white laboratory rat among aviary-based researchers interested in sexual selection and coloration, there is actually little evidence that UV signaling is of special importance to them. Zebra finches are certainly sexually dichromatic, but this is predominantly at longer wavelengths (e.g. reds and browns). In fact, the Zebra finch does not possess plumage colors with pronounced UV-reflectance peaks, its limited short wavelength reflection coming from the white plumage in which UV reflection is most likely simply a part of the broadband reflectance. In addition, the most important mate choice cues in this species are not UV-based, but instead song and red bill coloration (Burley and Coopersmith 1987; Collins and ten Cate 1996; DeKogel and Prijs 1996), and at least in some studies, females preferentially choose males wearing artificial red leg bands over those with orange, green or no leg rings (Burley 1982; Hunt *et al.* 1997).

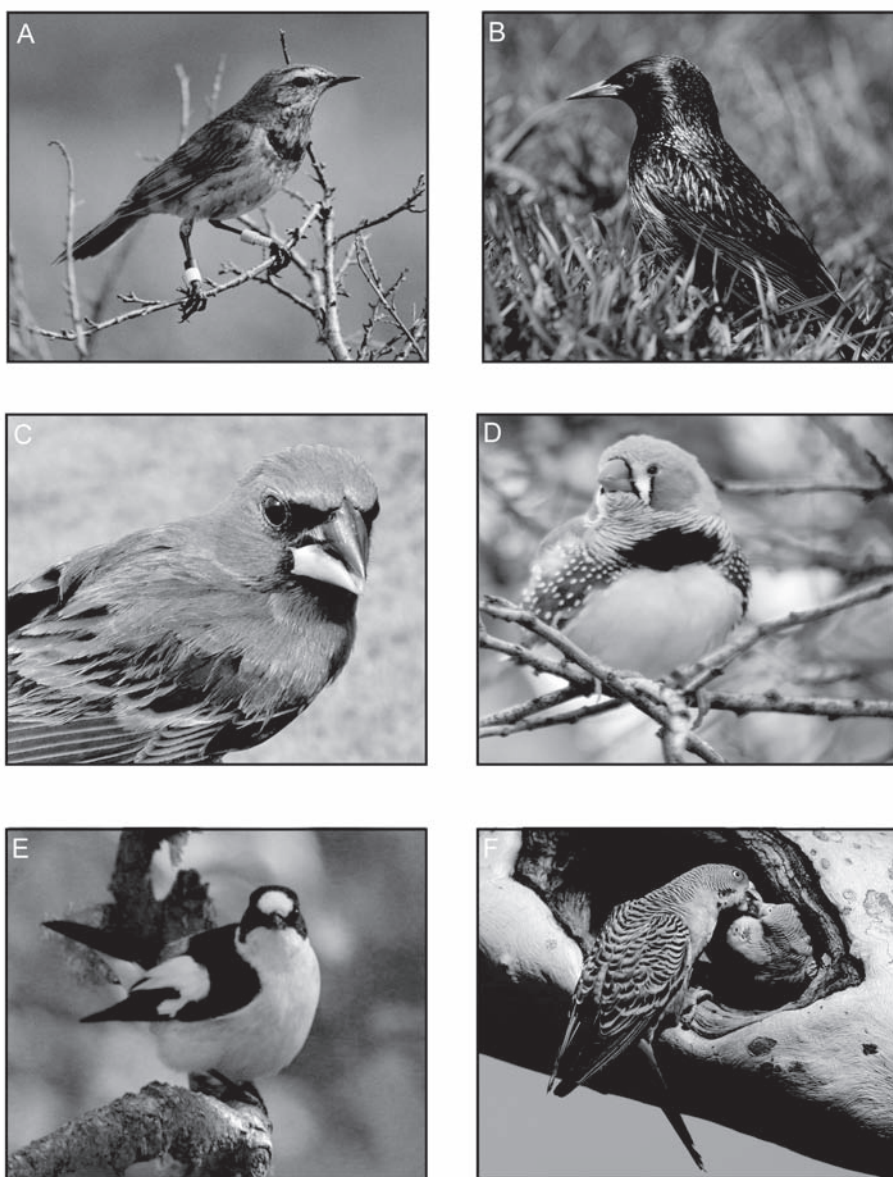


Fig. 1.6 Photos illustrating the diversity of sexually selected UV/structural and structural coloration among birds. **A.** The UV/blue throat patch of the Scandinavian Bluethroat, *Luscinia s. svecica*. Photo: Jonas Örnborg. **B.** The shimmering iridescent plumage of the European starling, *Sturnus vulgaris*. Photo: Tam Stuart. **C.** The bright UV/blue plumage of Eastern bluebirds, *Sialia sialis*. Photo: Mark Liu. **D.** The UV-reflective white plumage and red bill of the Zebra finch. Photo: Sarah R. Pryke. **E.** The white forehead patch of the Collared flycatcher, *Ficedula albicollis*. Photo: Thor Veen. **F.** The UV-reflectant and fluorescent cheek and crown patches of the Budgerigar, *Melopsittacus undulatus*. Photo: Sarah R. Pryke.

Table 1.1 Studies investigating the sexual function of UV/structural and structural color variation (size and/or intensity) in birds

Species	Ornament	Color measure	Study ^a	Manipulation	Sexual function	Outcome ^b	n	Reference
UV/Structural coloration								
<i>Erythrura gouldiae</i>	UV/blue	UV/blue	C		Female preference	+	96	Pryke and Griffith, unpubl. data
Gouldian finch					Male contest competition	+	85	Pryke and Griffith 2006
<i>Ficedula hypoleuca</i>								
Pied flycatchers	UV/brown	UV+/UV-	E	Oil	Female nest initiation	+	13	Sittari <i>et al.</i> 2002
<i>Guiraca caerulea</i>								
Blue grosbeaks	UV/blue plumage	UV/blue	C		Reproductive success	0	76	Keyser and Hill 2000
			C		Territory size and quality	+	36	Keyser and Hill 2000
			E	Blue/black marker pens	Female preference	0	11	Ballentine and Hill 2003
<i>Leiothrix lutea</i>	Body plumage	UV+/UV-	E	Filters	Mate preference	+	6	Maier 1993
Red-billed leiothrix								
<i>Luscinia s. svecica</i>	UV/blue throat	UV+/UV-	E	Oil	Male preference	+	16	Andersson and Amundsen 1997
Bluetheats								
	UV/blue throat	UV+/UV-	E	Oil	Female preference	+	63	Johnsen <i>et al.</i> 1998
	UV/blue throat	UV+/UV-	E	Oil	Extra-pair copulations	+	72	Johnsen <i>et al.</i> 1998
	UV/blue throat	UV/blue	C		Female preference	0	31	Smiseth <i>et al.</i> 2001
<i>Malurus cyaneus</i>	UV/blue plumage	Speed into nuptial molt	C		Extra-pair copulations	+	135	Dunn and Cockburn 1999
Superb fairy wrens								
<i>Cyanistes caeruleus</i>	UV/blue crown	UV/blue	C		Assortative mating	+	18	Andersson <i>et al.</i> 1998
Blue tits								

Table 1.1 Contd. ...

UV/blue crown	UV/blue	C		Female preference	+	7	Hunt <i>et al.</i> 1998
UV/blue crown	UV+/UV-	E	Filters	Female preference	+	6	Hunt <i>et al.</i> 1999
UV/blue crown	UV+/UV-	E	Oil	Female preference	+	41	Sheldon <i>et al.</i> 1999
UV/blue	UV/blue	C		Extra-pair copulations	-	49	Delhey <i>et al.</i> 2003
UV/blue crown	UV/blue	C		Adjustment of brood sex ratio over 3 years	+	86	Griffith <i>et al.</i> 2003
UV/blue crown	UV+/UV-	E		Male aggression towards mounts	+	24	Alonso-Alvarez <i>et al.</i> 2004
UV/blue crown	UV+/UV-	E	Oil	Female feeding rates	-	24	Limbourg <i>et al.</i> 2004
Structural body plumage	Green/bronze	E	Make-up powder	Female association	0	18	Mateos and Carranza 1995
Ring-necked pheasant		E	Make-up powder	Male dominance	+	12	Mateos and Carranza 1997
	Blue	E	Darkened/Lightened	Male territory defense	0	34	Stutchbury 1991
<i>Progne subis</i>							
Purple martins							
<i>Sialia sialis</i>	UV/Blue	C		Male reproductive success	+	16	Siefferman and Hill 2003
Eastern bluebird		C		Male nest box acquisition	+	35	Siefferman and Hill 2005b
		C		Assortative mating	+	218	Siefferman and Hill 2005a
<i>Sturnus vulgaris</i>							
European starlings	UV+/UV-	E	Filters	Female preference	+	16	Bennett <i>et al.</i> 1997
<i>Taeniopygia guttata</i>	UV+/UV-	E	Filters	Mate preference	+	8	Bennett <i>et al.</i> 1996
Zebra finches	UV+/UV-	E	Filters	Mate preference for UV versus other wavelengths	-	8	Hunt <i>et al.</i> 2001
Leg bands	UV+/UV-	E	Filters	Mate preference	+	14	Hunt <i>et al.</i> 1997

Structural coloration

Table 1.1 Contd. ...

Table 1.1 *Contd. ...*

<i>Anas acuta</i> Northern Pintails	Breast plumage	Whiteness	E		Female preference	+	36	Sorenson and Derrickson 1994
<i>Ficedula albicollis</i> Collared flycatchers	Forehead patch	Patch size	C		Lifetime reproductive success	+	75	Gustafsson <i>et al.</i> 1995; Sheldon and Ellegren 1999
			C		Male competition for nest boxes	+	30	Pärt and Qvarnström 1997
			E	Tippex	Male competition for nest boxes	+	110	Qvarnström 1997
			C		Extra-pair paternity	+	21	Sheldon <i>et al.</i> 1997; Sheldon and Ellegren 1999
<i>Ficedula hypoleuca</i> Pied flycatchers	Forehead patch	Patch size	C		Female preference (Spain)	+		Potti and Montalvo 1991
		Patch size	C		Female preference (Norway)	0	61	Dale <i>et al.</i> 1999
		Patch size	C		Male competition for nest boxes	0	33	Dale <i>et al.</i> 1999
<i>Gallinago media</i> Great snipe	White tails	Patch size	C		Female preference	+	53	Höglund and Lundberg 1987
			E		Female preference	+	26	Höglund <i>et al.</i> 1990
			E		Male competition	0	25	Höglund <i>et al.</i> 1990
		Whiteness	C		Female preference	0	79	Sæther <i>et al.</i> 2000
<i>Junco hyemalis</i> Dark-eyed junco	White tails	Patch size	E	Tail alterations	Male preference	+	24	Hill <i>et al.</i> 1999
<i>Poecile atricapillus</i> Black-capped chickadees	White plumage	Whiteness	C		Male dominance	+	40	Doucet <i>et al.</i> 2005
			C		Reproductive success (within and extra-pair)	0	38	Doucet <i>et al.</i> 2005

a. C = correlational study, E = experimental study where the signal is manipulated.

b. 0 = no relationship, - = negative relationship, + = positive relationship

Interestingly, although neither the red beak nor leg bands reflect strongly in the UV, the removal of UV-reflectance (via filters) affects female preferences for these traits (Bennett *et al.* 1996; Hunt *et al.* 1997). As mentioned above, this is probably because the filters alter the entire environment, including all the areas of the plumage, and hence change the overall appearance of the bird, as well as the contrast between different plumage areas.

Therefore, in order to test whether the effects of blocking UV in mate choice are in anyway unusual, Hunt *et al.* (2001) allowed female Zebra finches to choose among four males, each of which was seen through a different color filter. Filters were chosen to correspond with the peak sensitivities of the four Zebra finch retinal cone types, and therefore each male was seen to lack reflectance in either UV light, short-wave (perceived as blues and violets), medium-wave (perceived as greens) or long-wave (perceived as reds) human visible light. Rather than attending primarily to birds displaying stronger UV signals, females were least deterred by males lacking UV reflectance, and instead were affected more by the absence of red-reflecting wavelengths. This is not surprising given that most Zebra finch plumage has predominantly long-wave reflection and has very little reflection at short (including UV) or medium wavelengths (hence the greatest change in coloration will be produced by the removal of these longer wavelengths). One interpretation of earlier findings implicating the strong significance of UV in mate choice (e.g. Bennett *et al.* 1996) is that, in the light of this experiment, males simply exhibit more complete information about quality when viewed under the entire bird visible spectrum. It seems, therefore, that these birds do not rate UV-reflective signals as being any more instructive than those transmitted in other wavebands. As such, the Zebra finch is not, as commonly cited, a particularly appropriate role model for UV mate choice and more intriguing questions can instead be raised in more appropriate species.

1.5.1.2 Blue tits

One such species is the Blue tit, which provides one of the best studied examples of avian UV/structural sexual signaling to date. Blue tits are a socially monogamous species, but the incidence of extra-pair paternity is frequent enough (10-20% of offspring and 15-65% of broods; Kempenaers *et al.* 1992, 1997; Krokene *et al.* 1998) to cause substantial opportunity for increased sexual selection on males (see Chapter 8). As mentioned earlier, Blue tits were traditionally considered to show only a slight sexual dichromatism in blue crown color (Svensson 1992), but along with the development of reflectance spectrometry, the presence of both a large UV component and strong sexual dichromatism in the UV/blue plumage has now been documented (Andersson *et al.* 1998; Hunt *et al.* 1998; see Fig. 1.5).

There are several lines of evidence to suggest that the UV/blue crown is under directional sexual selection. In indoor mate-choice experiments, females seemed to prefer males with brighter UV/blue crowns (Hunt *et al.* 1998), and blue tits (of both sexes) viewed through UV-blocking filters were less preferred

than birds behind UV-transparent filters (Hunt *et al.* 1999). Free-living Blue tits also tend to mate assortatively with respect to the UV/blue crown coloration (Andersson *et al.* 1998), and territorial males adjust their aggressive responses depending on the UV/blue plumage of conspecifics (Alonso-Alvarez *et al.* 2004). Furthermore, male coloration may actually act as an indicator of the expected value of the offspring. This idea is supported by the finding that females produce more male offspring when mated to males with highly UV/blue chromatic plumage, whereas low UV/blue saturated males tend to have more daughters in their broods (Sheldon *et al.* 1999; Griffith *et al.* 2003). When the UV-reflective component of the males' crowns was blocked (with UV-absorbing sunblock; see Fig. 1.5), this relationship was reversed (Sheldon *et al.* 1999), providing the first experimental demonstration that female birds manipulate the sex ratio of their brood in relation to the attractiveness of their partner (Fig 1.7). The apparent female perception that males with highly UV-reflectant crown plumage are higher-quality mates is highlighted by the finding that these males have a much higher level of over-winter survival (Sheldon *et al.* 1999; Griffith *et al.* 2003). This is consistent with an earlier study (which did not measure color) demonstrating that males with high survival prospects achieve higher seasonal reproductive success by

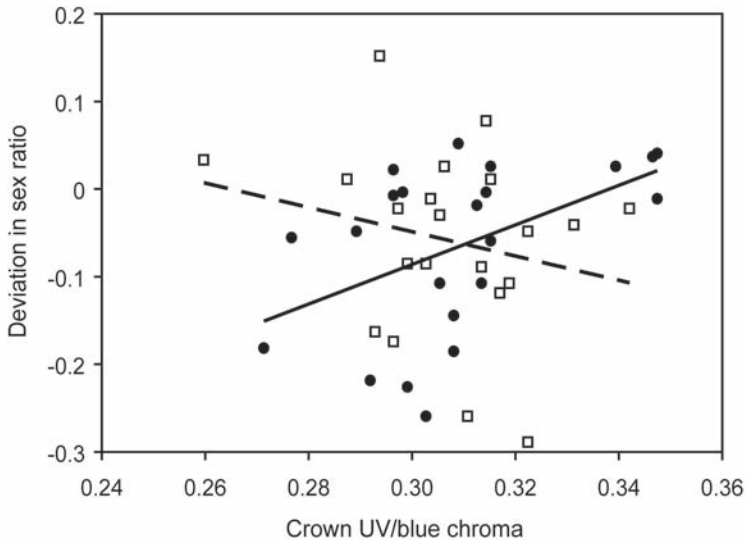


Fig. 1.7 The sex ratio of Blue tit broods from males with UV-reduced (coated with sunscreen) crown plumage (dashed lines, open symbols) and control UV-reflectant birds (continuous lines, closed symbols). Females paired to males with UV-reflective blue crowns produced more male offspring than those paired to males with no UV in their plumage. Redrawn from Sheldon *et al.* 1999. *Nature* 402: 874-877, Fig. 2.

being cuckolded less and siring more extra-pair offspring (Kempnaers *et al.* 1997).

However, even the function of the UV/blue plumage in this well-studied system is not without its problems. For example, despite the increased variance in male reproductive success and strong effects of male UV/blue ornamentation on male reproductive success (both within-pair and extra-pair paternity), the actual net directional selection on male UV/blue crown color may be relatively weak (Delhey *et al.* 2003). Although females tend to be more faithful to males with more intense UV/blue crowns, less UV-ornamented males may achieve higher extra-pair success (Delhey *et al.* 2003), suggesting that the UV/blue plumage is only likely to be one, among a number of variables used in female mating decisions. Perhaps the expression, effectiveness and relative importance of this signal varies both spatially (i.e. geographically; see Andersson *et al.* 1998; Hunt *et al.* 1998) and temporally (i.e. seasonally; Griffith *et al.* 2003), with different selective pressures (e.g. sexual and/or natural) favoring separate traits under different conditions. Nevertheless, the sexually dichromatic UV/blue crown of Blue tits provides one of the best demonstrated examples of a sexually attractive UV/structural signal.

1.5.1.3 Bluethroats

Another socially monogamous European bird, the Bluethroat (*Luscinia svecica svecica*), has become a traditional example for UV/blue plumage functioning in sexual selection (Fig. 1.6). In the first experiment to manipulate a natural UV/structural plumage ornament in isolation, Andersson and Amundsen (1997) compared preferences of female Bluethroats for males whose UV/blue throat patches had been treated with oils either containing sunblock (no UV) or a black pigment (with UV, but also controls for the elevated effects of UV-removal on signal brightness). Females strongly preferred to associate with males displaying a blue UV-reflective throat patch over those with non-UV-reflective plumages. Using the same manipulation in the field, Johnsen *et al.* (1998) found that male Bluethroats with UV-removed patches had much lower success in attracting females and in achieving extra-pair copulations, and were cuckolded more frequently than males displaying UV-reflective throat patches. However, it is noteworthy that within the natural range of plumage reflectance, a female preference has yet to be demonstrated (Johnsen *et al.* 2000; Smiseth *et al.* 2001), and that the UV-reduction treatments (Andersson and Amundsen 1997; Johnsen *et al.* 1998) far exceeded the natural variation (i.e. completely removed UV). This suggests that strong treatment (i.e. supernormal) effects are required in order to produce a detectable sexual response from females and perhaps to overcome other important factors. Thus, while the above experiments show that UV cues in plumage do affect mate choice, they do so only in the sense that completely removing them adversely affects female preferences.

1.5.1.4 Recent UV/structural studies

More recently, other studies have begun to explore the sexual signal function of UV/structural plumage in a range of species, with varying results (see Table 1.1 for full summary). For example, in Eastern bluebirds (*Sialia sialis*) more intense UV/blue plumage (see Fig. 1.6) is important in resolving male conflicts over nest boxes (Siefferman and Hill 2005b) and is associated with male mating success (fledglings raised) in the field (Siefferman and Hill 2003). Similarly, in females, UV/blue color expression is related to the timing of breeding and quality of the offspring produced (Siefferman and Hill 2005a). Although these birds mate assortatively on the basis of this plumage cue (Siefferman and Hill 2005a), the direct mechanism of sexual selection (i.e. male, female and/or mutual) is unknown. In another species, the Blue grosbeak (*Guiraca caerulea*), the UV/blue plumage is important in determining aspects of territory quality (Keyser and Hill 2000), but females demonstrate no preference for the relative UV/blue plumage of males, either within the natural variation in the field (Keyser and Hill 2000), or when manipulated in captivity (Ballentine and Hill 2003). In other systems, such as that of the color polymorphic Gouldian finch (*Erythrura gouldiae*), the brilliant UV/blue plumage is just one of many striking plumage colors (see Fig. 1.2), yet it is important in both female mate choice and male competition (Pryke and Griffith 2006). During male contests among birds of the same color morph, males with more chromatic UV/blue collars are dominant to birds with less intensely colored collars. Similarly, in mate choice experiments, females (of all morphs) prefer males (of all morphs) with more saturated UV/blue head collars. These strong sexual effects are despite the presence of a large number of other color ornaments (Fig. 1.8).

Although clearly still in its early stages, avian behavioral research has shown that variation in the UV component of UV/structural coloration can function as a signal to conspecifics. Interestingly, these studies also suggest that relatively small differences in UV reflectance could be detected and perceived as distinct colors by the avian visual system. Indeed, behavioral studies in Blue tits (Andersson *et al.* 1998; Hunt *et al.* 1998), European starlings (Bennett *et al.* 1997) and Bluethroats (Andersson and Amundsen 1997) have demonstrated that differences in UV plumage reflectance of as little as 5% can influence intraspecific interactions. The biological significance of these small UV differences implies that there is potentially a huge amount of information available in these signals to birds.

1.6 SEXUAL SELECTION AND STRUCTURAL SIGNALS

Most behavioral studies of structurally-based plumage have focused exclusively on the UV component. This is not surprising, given that UV-reflectance is typical in many structurally-based plumage colors, and the recent discovery of the importance of UV in the lives of birds. Nevertheless, there are a few, albeit limited, studies investigating the signal function of

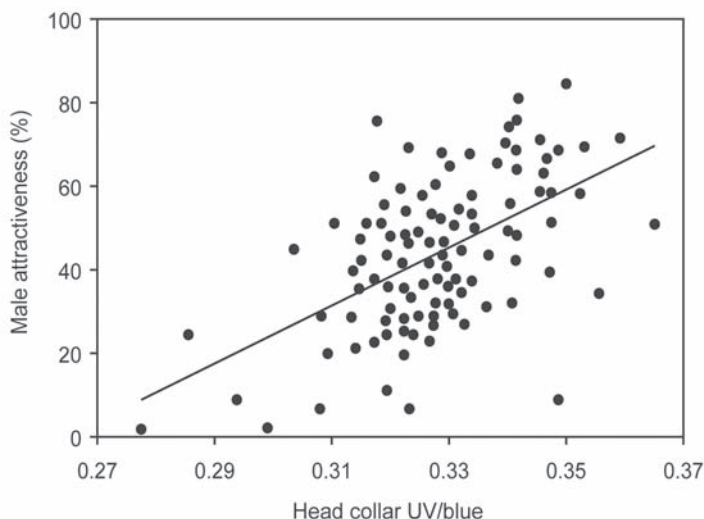


Fig. 1.8 The relationship between UV chroma of the UV/blue head collar of Gouldian finches, *Erythrura gouldiae* (see Fig. 12.2) and male attractiveness ($n = 104$). Females strongly preferred males displaying more saturated (i.e. chromatic) UV/blue collars over less intensely colored males. Original.

structural plumages (without an important UV component) (see Table 1.1). Of these, white plumage is probably the most common and widespread among birds. Yet, white plumage patches have been largely overlooked, especially in the context of structurally-based coloration. This is presumably because of the limited variation in the spectral properties or ‘color’ of most white plumages (but see Doucet *et al.* 2005). Nonetheless, a number of studies have shown that white plumage patches are important in sexual selection, although generally it is the size of the white patch rather than qualitative variation in reflectance that is the important signal parameter (see Table 1.1). Perhaps the best studied example of sexual selection in an avian species is the Collared flycatcher (*Ficedula albicollis*), with its conspicuous white forehead patch.

In particular, a breeding population of Collared flycatchers in Sweden has been the subject of intense long-term study since 1989 (Gustaffsson 1989; Gustafsson *et al.* 1995; Qvarnström 1998, 1999; Qvarnström *et al.* 2000), with most studies directed at investigating the sexual signaling function of the white forehead patches (Fig. 1.6). Using a combination of observational and experimental approaches in the field, it has been shown that a wide range of selective mechanisms act on the variation in the size of the male’s white forehead patch. Experimentally staged contests between males have shown that forehead patch size is the best phenotypic predictor of the outcome of disputes over territory ownership (Pärt and Qvarnström 1997), and experimental manipulations of forehead patch size have demonstrated that males trade-off effort spent in male competition with effort in paternal care

(Qvarnström 1998). Manipulations of paternal care (by changing brood size) have revealed that this trait is condition-dependent, since males given more young to rear return in the following year with smaller patches, whereas males given fewer young return with larger patches (Gustafsson *et al.* 1995; Griffith and Sheldon 2000), and young reared in experimentally enlarged broods have smaller patches than those reared in reduced broods (Gustafsson *et al.* 1995). Although these experiments reveal that a large proportion of variation in badge size can be explained by variation in individual condition, cross-fostering experiments suggest that the trait is also heritable and reflects genetic benefits to the offspring (Sheldon *et al.* 1997). Consistent with this genetic component to the variation in forehead size, the sex ratio of offspring is skewed in favor of sons when females are mated to large patched males, and in favor of daughters when mated to small patched males (Ellegren *et al.* 1996). In addition, paternity analyses have shown that small patched males are more likely to be cuckolded, and that large patched males are more likely to father these extra-pair offspring, contributing significantly towards variance in reproductive success amongst males (Sheldon and Ellegren 1999). Overall, studies of the white forehead patch have revealed a highly complex and seasonally adaptive female preference for male forehead size (Qvarnström *et al.* 2000).

1.7 SEXUAL SELECTION AND FLUORESCENT SIGNALS

To date, the only studies of fluorescence in sexual communication have focused on the Budgerigar (*Melopsittacus undulatus*). Both sexes have fluorescent yellow plumage on their crown and cheeks that they use in courtship displays (Fig. 1.6). In mate choice trials, birds presented with conspecific birds of the opposite sex whose plumage had been manipulated with either sun block (Fluorescent-present) or petroleum jelly (Fluorescent-absent) demonstrated a sexual preference for fluorescent conspecifics (Arnold *et al.* 2002). In contrast, other studies using filters to selectively block fluorescence from UV light showed that, while Budgerigars preferred mates when viewed in UV light, the loss of fluorescence did not affect mate attractiveness (Pearn *et al.* 2001, 2003). Subsequently, the relative importance of fluorescence signals in sexual selection, both within the budgerigar and other species, is unknown.

Furthermore, it is unknown what, if anything, fluorescent patches are signaling. Most likely, fluorescent patches are simply by-products of pigment structure. Although, the widespread occurrence of fluorescent signals among parrots, and their appearance, often alongside UV-reflecting signals, in traits which are used in courtship displays, implies that they may potentially be important in signaling (Hausmann *et al.* 2003). One possibility is that by absorbing UV light, fluorescent pigments can enhance contrast with nearby UV-reflecting plumage, thereby increasing conspicuousness in the UV waveband (Pearn *et al.* 2001). In the Budgerigar, for example, the UV-absorbing fluorescent yellow crown and cheeks will contrast with the UV-reflecting

yellow throat and facial areas, and with the UV-blue cheek patches (Hausmann *et al.* 2003; Pearn *et al.* 2003). However, at present, too little is known and further studies on different systems are needed.

1.8 WHY ARE UV/STRUCTURAL SIGNALS USED IN SEXUAL COMMUNICATION?

As discussed above, some birds do use UV-reflective plumage as cues in sexual communication, however, debate has arisen as to whether these signals play a 'special' role in sexual communication (Cuthill *et al.* 2000; Banks 2001; Hunt *et al.* 1997; Hausmann *et al.* 2003). There are a number of plausible reasons why birds may use UV/structural signals over those of longer wavelengths. Here I will consider five possible, but not mutually exclusive, hypotheses. The first three are based on the idea that there is something particularly suitable about the short wavelengths for signaling, while the remaining two are based predominately on current honest-enforcing sexual selection theory.

1.8.1 Private Signaling Channel

One explanation is that the UV waveband may provide a secret or private channel for communication among only the intended receivers. There are two main possibilities in this case. First, UV signals have been suggested to constitute a secret avian channel, allowing birds to signal to conspecifics without being conspicuous to mammalian predators who are unable to perceive UV light (Jacobs 1993; Guilford and Harvey 1998). Second, because shorter wavelengths scatter more readily than long wavelengths (Lythgoe 1979; Andersson 1996), the UV may be a better wavelength for signaling over short distances. That is, a bird could use plumage conspicuous in the UV to display to a nearby mate or rival, yet avoid the costs of being simultaneously conspicuous to illegitimate receivers or eavesdroppers over longer distances (e.g. aerial predators). However, while these remain appealing arguments, they are yet to be supported by experimental results.

1.8.2 Light and Habitat Contrast

Another explanation is that UV-reflecting signals may create a particularly strong contrast between the trait/bird and its environment. In addition to the difference between short and longer wavelengths over distances, the relative intensity of UV versus longer wavelengths also varies dramatically across a number of other contexts. Ultraviolet light is relatively strong at dawn and dusk, when the sun's low angle allows the atmosphere to absorb longer wavelengths and scatter shorter ones. Open, less vegetated habitats are richer in UV light because chlorophyll absorbs UV wavelengths of light (Endler 1993). On cloudy days, UV's relative intensity increases, and UV is stronger at higher altitudes due to the thinner atmosphere (Lythgoe 1979). Other factors that may influence the quality of UV light include everything from latitude,

season, and lunar phase to the reflectance of different rock and soil types (Chittka *et al.* 1994). Since sexual signaling theory predicts that birds should produce the most efficient signals, with maximum conspicuousness for the signaling conditions (Andersson 2000), it seems likely that they will use signals or displays in the most effective lighting contexts (e.g. Endler 1993). In agreement with this, recent work on birds has shown that males typically choose appropriate sites and times of day that maximize the conspicuousness of their color displays (Andersson 2000; Andersson *et al.* 1998). For example, the Blue tit inhabits woodlands and typically displays in more shaded areas, where its UV-reflective blue crown is especially conspicuous against the UV-deficient vegetation (Andersson *et al.* 1998). Similarly, Bluethroats display before sunrise and after sunset, during the long dawn and dusk which is typical of Scandinavian altitudes (Andersson 2000). In clear conditions, this allows displaying birds a relatively long period of short-wavelength-rich light, which when coupled with the typical brown alpine habitat in spring, enhances the conspicuousness of the Bluethroats' UV/blue plumage (Fig. 1.6).

However, birds behaviorally enhancing the conspicuousness of their displays to their environment is not restricted to UV-reflective signals. Other color displays, such as white structural color patches provide a particularly striking contrast in darker habitats. This is well illustrated in a comparative study of eight Leaf warbler species (*Phylloscopus* spp.) occupying a range of habitats from low montane scrub to broadleaf forest (Marchetti 1993). All eight species are primarily yellow-green but vary in the number of white color patches on the wings, head and rump—the darker the habitat, the more patches of white they possess. Similarly, the brilliant blue and white patches of male White-throated manakins (*Corapipo gutturalis*) are enhanced by a high brightness contrast in their display environment (Théry and Vehrencamp 1995). The males form small leks deep within tropical forests where they display to females from fallen logs on the forest floor. The appearance of sunlight through gaps in the forest canopy stimulates males to display, with their color patches enhanced by the high brightness contrast between the lekking arena (with sunlight) and the surrounding dark understorey.

1.8.3 Receiver Biases for UV-Reflective Signals

An alternative possibility is that UV signals have evolved via receiver biases (i.e. sensory exploitation) to utilize pre-existing avian preferences for UV-reflective signals. For example, it has been suggested that birds are particularly sensitive to UV wavelengths of light compared with other wavelengths (Burkhardt and Maier 1989) and that birds developed UV vision primarily in order to navigate (see Vos Hzn *et al.* 1994) and/or find food (see Church *et al.* 1998). In either case, it is possible that, similar to the findings from other sexual signals (Ryan 1990; Endler and Basolo 1998), UV signals could be favored because birds are predisposed to such signals. Unfortunately, experimental tests investigating the importance of UV signals

in receiver biases, alone or relative to other environmental and adaptive selective mechanisms, have not yet been undertaken.

1.8.4 Signals as Amplifiers of Mate Quality

A different idea is that UV and structural signals may act, not as quality-indicating signals *per se*, but rather as amplifiers of behavior (Fitzpatrick 1998). Amplifier signals are not functionally related to the quality being signaled, instead, the amplifier simply makes it easier for the receiver to assess that quality, i.e. reliability is enforced by design (efficiency) rather than direct costs (Hasson 1989, 1991). For instance, a number of UV-reflective patches in parrots are invariably found alongside strongly fluorescing patches (Hausmann *et al.* 2003), which together increases the relative chromatic contrast of the plumage, leading to greater signal efficiency (Hausmann *et al.* 2003). Likewise, many UV signals are also iridescent. Perhaps such iridescence increases the receiver's accuracy of judging the vigor, precision or quality of the behavior or individual. Once again, at this stage, there is little empirical support for this idea and tests are needed.

1.8.5 Signals as Indicators of Mate Quality

Lastly, UV/structural signals may be particularly sensitive indicators of some type of quality. Current sexual selection theory suggests that sexual ornaments have evolved to honestly signal aspects of mate quality, where individuals expressing the most extreme expression of the ornament will enjoy a fitness advantage, either for themselves or their offspring (Andersson and Iwasa 1986; Zahavi and Zahavi 1996; Chapter 5). Most UV-reflective and structural plumage signals are created by the microstructure of the feathers rather than pigmentation (see above), and recent work within this microstructure has provided a few clues that structural coloration may be an unusually good indicator of feather quality. In particular, these costs may be reflected in the thickness and regularity of the feather nanostructure (Fitzpatrick 1998; Andersson 1999). For example, the differential ability of individuals to produce a regular structure (i.e. variation in the number and size of keratin rods within the medullary layer of the feather barbs) may determine the variance in the observed color (Shawkey *et al.* 2003). That is, birds who express more saturated UV/blue plumage, such as the Eastern bluebird, tend to have more keratin rods, which also vary less in size, than duller birds (Shawkey *et al.* 2003). Assuming that there is some cost involved in producing a greater number and more uniform keratin rods (e.g. nutrition during molt), this could possibly provide an indicator mechanism of structural plumage.

Another potential cost of feather microstructure is the trade-off between the investment into the optimal feather shape to best amplify the UV or structural signal (Andersson 1999) and the feather shape most efficient for thermoregulation. The maintenance of UV/structural plumage might also

incur costs. For instance, abrasion of the barbs containing the color structure is likely to affect the resulting colors. This occurs in Blue tits, whose plumage changes from a highly intense UV-reflective signal just after molt to a duller and less chromatic UV signal later in the year (Örnborg *et al.* 2002). Examining the feathers of these birds demonstrates a significant wear on the feather barbs (Fig. 1.9). Hence, costs of keeping the plumage in good condition (e.g. preening, finding shelter and food) may affect the color and mediate honest signaling of phenotypic quality. It should be noted, however, that most of these presumed costs discussed above are still speculative and there is very little unequivocal evidence that structural feathers invoke strong production costs on plumage displays, although this almost certainly reflects the early stage of research in this area (which is currently growing) rather than its relative importance.

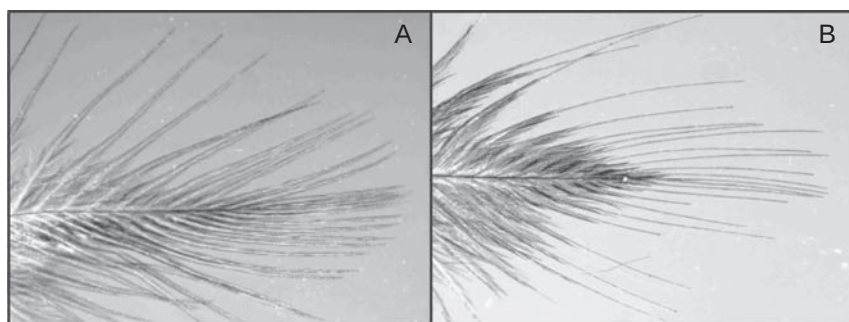


Fig. 1.9 Digital images of male blue tit crown feathers illustrating the differences in quality of two feather barbs. Feathers were sampled at two different seasonal times: **A.** just after molt and **B.** during nestling feeding. Photos: Jonas Örnborg.

Similar to other mechanisms of color production, a number of condition-related qualities have also been proposed for UV/structural coloration. The use of structural colors as condition-dependent indicators is perhaps less intuitive than those of other colors, such as pigment-based melanin and carotenoid signals (see Chapter 2), whose expression typically invokes a number of direct costs (e.g. foraging ability, parasite-inhibited uptake and competing physiological functions; Olson and Owens 1998). Nevertheless, at molt into their brilliant coloration, the expression of structural signals (like other signals) is likely to reflect an individual's overall general condition (i.e. an interaction of all aspects of genetic quality, health and life-history). One of these indices, nutritional condition during molt, has been suggested to explain the variance in structurally-based coloration in Blue-black grassquits (Doucet 2002) and Blue grosbeaks, *Passerina caerulea* (Keyser and Hill 1999). However, these studies examining the correlations between relative color expression and feather growth rate provide little evidence that nutritional status is directly involved in coloration. To test this idea experimentally, McGraw *et al.* (2002) subjected male Brown-head cowbirds, *Molothrus ater*, to

periods of fasting during the molt into their bright iridescent plumage. Birds which were more nutritionally stressed, grew less green, less saturated and less bright iridescent plumage than undeprived birds. Similarly, a recent food-deprivation experiment also demonstrated that the UV/blue plumage of female Eastern bluebirds is affected by nutrition during molt (Siefferman and Hill 2005a). One problem with such experiments, and one which is not limited to studies of structural coloration, is that food restriction experiments will undoubtedly affect condition, and thus the subsequent influence on the expression of sexual color signals may be secondary effects caused by a number of unknown mechanisms. As such, it is problematical to explicitly invoke a direct relationship between diet and color expression in such experiments (see Griffith and Pryke 2006).

Another commonly invoked, albeit rarely unequivocally demonstrated, condition-related quality is the potential link between parasite resistance and color in birds (Hamilton and Zuk 1982), given that females choosing bright males would gain partners who signaled their resistance to parasites and would also presumably be in better overall condition. In UV/structural plumages, relationships between the intensity of parasite infection and the expression of the UV/blue iridescent plumage of Satin bowerbirds (*Ptilonorhynchus violaceus*) (Doucet and Montgomerie 2003) and the UV component of red combs in the Red grouse (*Lagopus l. scotius*) (Mougeot *et al.* 2005) have been described. Yet, the correlative nature of these studies does not reveal whether colorful males have higher levels of resistance to parasites or have simply escaped exposure to them. More convincingly, male wild Turkeys (*Meleagris gallopavo*) severely infected with coccidial oocysts (*Eimeria* spp.) molted into a less intense UV/iridescent plumage than uninfected males (Hill *et al.* 2005). However, in this case the selective mechanisms have not been identified, and therefore the relative importance of plumage coloration, and its condition-dependence, in sexual selection are unknown.

Physiologically-controlled mechanisms such as hormones may also play a direct role in mediating structurally-based plumage. For example, testosterone affects the speed of males acquiring breeding plumage in Superb fairy wrens (*Malurus cyaneus*) (Peters *et al.* 2000), a species arguably displaying one of the most brilliant and chromatic UV/blue plumages among birds. In these champions of sexual infidelity, males which molt faster from their drab-brown non-breeding plumage into their bright blue breeding plumage also gain more extra-pair paternity (Dunn and Cockburn 1999). Although molt speed is thought to be related to male condition (Mulder and Magrath 1994), unfortunately neither the quality nor the variation of this UV/blue plumage has been measured, and as such the relative importance of this color in sexual selection remains unknown.

Finally, coloration may simply be used to signal overall condition and health of the birds. This is suggested by the survival rate of overwintering Blue tits where males with more chromatic UV/blue plumage are more likely to survive to the next breeding season than less chromatic birds (Griffith *et al.*

2003; Sheldon *et al.* 1999). Furthermore, a recent study on fledgling condition (i.e. body mass) suggests that the UV/blue plumage may be related to condition (Johnsen *et al.* 2003). Similar to the adults, Blue tit nestlings are sexually dichromatic in the expression of UV/blue plumage, and heavier nestlings display more chromatic blue tails with a larger UV component (Johnsen *et al.* 2003). The adaptive significance of sexual dichromatism in nestling birds is unknown, but potentially, if the condition-dependence of nestling plumage coloration translates into future adult condition and fitness, this may provide an avenue for condition-dependence of structural plumage. However, this remains to be demonstrated.

The above studies highlight not only the potential direct costs which structural plumage could invoke, but also the large gaps in our understanding of these costs. As yet, no studies have explicitly shown that birds raised under a range of different conditions will have different structural colors in their feathers, which in turn are important for choosy females. While at this stage it seems reasonable to expect a relationship between structural color and sexual condition, this is obviously an area in need of further investigation.

With these limited indications of honest signaling, there are few clues to the benefits of female choice based on structural colors. It is interesting, however, that in a comparative study by Owens and Hartley (1998) it was found that the frequency of extra-pair copulations covaried with sexual dichromatism based on structural, but not melanin or carotenoid coloration. In addition, a more recent comparison of a number of avian families across mainland Australia, provides further behavioral evidence for an important mate choice function of UV-reflecting plumage (Hausmann *et al.* 2003). Out of 108 species surveyed, 72% possessed an UV component in their plumage, suggesting that UV displays are typical signals in avian plumages (see also Eaton and Lanyon 2003; Eaton 2005). Notably, while there was no association between long- and medium-wave plumage colors (e.g. yellow and reds) functioning in courtship displays, there was a strong bias for body regions containing UV-based plumages to be used in courtship displays. This is clearly a fruitful area for further investigation, and future studies of mate choice based on UV and structural coloration may prove to be especially interesting.

1.9 FUTURE CHALLENGES

Traditionally, coloration has played a key role in the study of visual signaling and in the burgeoning field of sexual selection. Yet, until recently, an entire color channel, that of the UV, has been ignored, potentially undermining the vast literature on sexually selected avian color signals. Thus, the recent discovery of UV in the lives of birds has led to the expectation of a particularly important function for UV in sexual communication. However, despite the surge of studies over the last ten years, there is little direct evidence to support this notion. Indeed, while UV-reflecting plumage is both

widespread and typical among bird taxa (Eaton and Lanyon 2003; Hausmann *et al.* 2003; Eaton 2005), most plumage UV reflectance is probably an unselected consequence of its chemical and physical structure (Andersson 1996, 1999). Neither have human invisible, and thereby likely adaptive, UV patterns been demonstrated in birds. Such secret signals are known only in flowers (Silbergleid 1979) and possibly lizards (Fleishman *et al.* 1993). In fact, UV is in most cases a strongly correlated extension of the spectra that we humans can see, and likewise, presumably birds are not viewing UV in isolation from other color signals.

Nevertheless, this does not detract from the possible significance of UV to birds. UV color vision allows birds to see not only a greater range of wavelengths, but also permits greater discrimination of colors, even within the human visible waveband. In addition, UV colors may be particularly effective for signaling (Andersson 1996, 1999; Bennett and Cuthill 1994), conspicuously contrasting with other plumage traits and habitat backgrounds, while simultaneously remaining hidden from more distant or UV-blind predators and eavesdroppers. However, caution needs to be taken when assuming that UV signals are anymore 'special' than other signals. In fact, a key finding from this review is that despite major advances in this field, and a general belief that UV signals are likely to be a particularly important component of bird coloration, few studies have explicitly demonstrated this. At this stage it seems logical that the UV waveband is important for birds, especially certain crepuscular species (e.g. Blue tits and Bluethroats), although perhaps less special than first imagined for many species such as the diurnal Zebra finches where there is little evidence that UV information is any more important than signals in other wavebands (Hunt *et al.* 2001). Indeed, while UV/structural coloration is often viewed as a separate entity from that of other types of coloration, such as melanin and carotenoid-based pigmentation (e.g. as evidenced by the devotion of two separate chapters in this book), presently, there is insufficient empirical support to identify qualitative differences between the different color mechanisms in the evolution of bird plumages. Thus, whilst this remains an appealing (and perhaps likely) distinction, further studies are needed to investigate the relative importance of UV/structural signals to those of other sexual signals, both color and other potential sexual cues, in sexual communication among birds.

Overall, whilst the limited empirical work in this area provides us with the very basic summary, the majority of studies are descriptive in nature and are unable to unravel the interactions between UV and structurally-based signals and the suite of other traits involved in sexual selection. Even the more experimental work is generally quite limited in its scope (e.g. gross-level manipulations) and has been tackled in a very small number of species. As a result, a number of questions, fundamental to understanding signaling function and behavior, are still to be properly addressed. For example, to what extent is the UV reflectance in plumage an adaptive signal rather than simply

a by-product of feather structure? Have habitat/light differences affected the evolution of different plumage colors? As such, what is the relative importance of light environments, foraging efficiency and direct mate assessment in the evolution of UV-reflective signals? As highlighted above, are UV/structural displays more likely to be the focus of sexual selection than pigment-based colors? Similarly, what are the relative production and maintenance costs (including signal exploitation through predators and eavesdroppers), and how do these relate to different dimensions of UV/structural signals? What are the fitness consequences to birds expressing UV/structural plumage? Given the advanced tools that we now have at our disposal (e.g. field portable reflectance spectrometers and molecular tools), together with the increasingly clever experimental and statistical innovations, we are now in a better position than ever before to provide some exciting answers into this fascinating area of avian biology.

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Melanins and Carotenoids as Feather Colorants and Signals

Geoffrey E. Hill

2.1 INTRODUCTION

The signal function of ornamental traits has become a focus of intense interest by behavioral and evolutionary biologists. Ornamental traits posed among the greatest challenges to Darwin's theory of natural selection (Cronin 1991) because they seemed to decrease survival while not directly enhancing fecundity. Darwin solved this problem by devising his theory of sexual selection whereby traits like ornamental coloration evolved because they enhanced access to mates through mate attraction or success in intrasexual competition (Darwin, 1871). Darwin proposed that female mate preference was primarily responsible for the evolution and maintenance of ornamental coloration in birds. While Darwin (1871) correctly solved the primary dilemma of how ornamental coloration evolved, he left many questions unanswered including what ornamental traits signal to conspecifics.

In this chapter I will consider the signal function of pigment-based feather coloration focusing on several overarching questions that unite most current research: What is the proximate basis for variation in color displays in birds? What is the function of ornamental plumage coloration? If ornamental coloration functions as a signal, what information is encoded in the color display? Is there evidence that individuals benefit by assessing color signals? There are currently no comprehensive and universal answers to these questions. In recent years, however, we have learned an enormous amount about the proximate controls and signal function of the color displays in bird plumage, and I will work from this base of information in considering the questions that I pose above.

I will focus on coloration that results from the deposition of the two most common and best-studied plumage pigments: melanins and carotenoids. Melanin pigmentation is ubiquitous in birds. Melanins serve as colorants in

the feathers of all but handful of all-white species (McGraw 2006b). Two types of melanin pigments serve as feather colorants—eumelanins, which produce the bold black patches displayed by many species (Fig. 2.1) as well as an enormous variety of black spots, bars, bands, and stripes, and phaeomelanins, which produce earth tone coloration that can vary from yellow to reddish to brown (McGraw 2006b). Much more research has been conducted on both proximate control and function of eumelanin pigmentation compared to phaeomelanin pigmentation, so I will restrict my treatment to eumelanins. Carotenoid pigments are not quite as ubiquitous in birds as are eumelanin pigments, but carotenoids are responsible for many of the bright yellow, orange, and red plumage color displays in species in many avian orders and families (Fig. 2.1; McGraw 2006a).

Dale (2006) proposed that plumage coloration potentially communicates seven types of information: quality, attractiveness, strategy, genetic compatibility, kinship, individual identity, or presence. These are not necessarily mutually exclusive signal functions, but the primary function of a color trait is expected to determine how that color display is distributed across individuals in a population (e.g. normal, polymodal, or uniform), how it is related to individual quality (e.g. condition or dominance), and how complex or simple the trait is (Dale 2006). In my treatment of melanin and carotenoid coloration I will focus on plumage coloration that has been shown to be or appears to be ornamental. By the terminology of Dale (2006), focusing on ornamental color displays means that I will exclude signals of presence and, in particular, plumage color that appears to function primarily in crypsis. I will also not consider genetic compatibility or kinship in this chapter (see Mays and Hill (2004) for a discussion of why plumage coloration is unlikely to signal genetic compatibility within populations). My primary focus will be on signals of quality, attractiveness, and strategy, which are the signal functions that are the focus of the literature on avian coloration. I explain what is meant by signals of quality, attractiveness, and strategy below.

To understand the signal content of ornamental plumage pigmentation, it is essential to understand the factors that shape variation in expression of the trait. For this reason, I begin with a brief review of the proximate mechanisms that produce carotenoid and eumelanin coloration in feathers. I then present our current understanding of the degree to which genes and the environment shape the expression of carotenoid and melanin plumage coloration. I conclude with a brief review of how carotenoid and melanin plumage coloration function and a consideration of how such traits might serve as useful signals to conspecifics.

2.2 MECHANISMS OF PRODUCTION OF MELANIN AND CAROTENOID COLORATION

Melanin pigments are large polymers with repeated indole subunits (benzene and pyrrole rings) that cross link into complex macromolecules (Fox and Vevers (1960); Fig. 2.2). Melanins are synthesized by birds from the amino acid

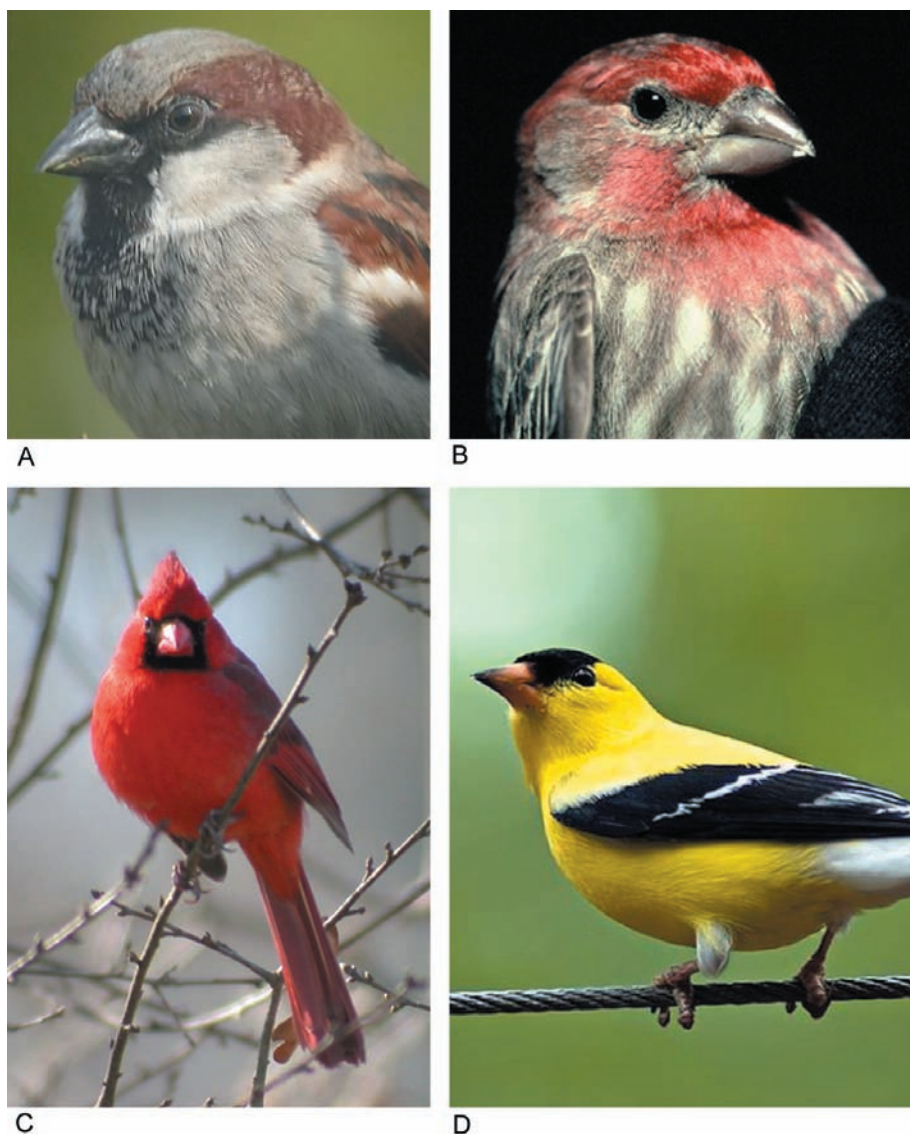


Fig. 2.1 Much of the ornamental coloration of birds results from melanin and carotenoid pigmentation. **A.** Male House sparrows have melanin-based black throat patches. **B.** Male House finches have carotenoid-based red plumage coloration. **C.** Northern cardinals and **D.** American goldfinches have both red/yellow carotenoid coloration and black melanin coloration in their plumages. Photos A. Ian Forrest, B. Geoffrey Hill, C. Mark Liu, D. Todd Adamson.

tyrosine. Tyrosine can be ingested and used directly to produce melanin or tyrosine can be produced from phenylalanine or cysteine (see McGraw, (2006b) for a detailed account of melanin synthesis in birds). Thus melanin is

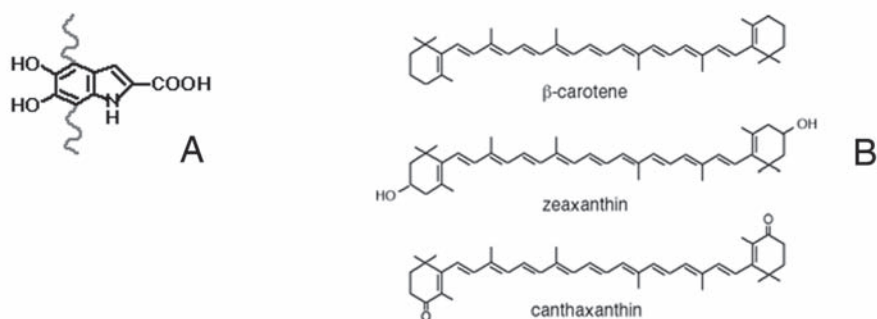


Fig. 2.2 **A.** The chemical structure of the indole backbone of eumelanin. Indoles are covalently linked into polymers to form melanins. **B.** The chemical structure of three major classes of carotenoids. β -carotene is classified as a carotene because it is composed only of carbon and hydrogen with no hydroxy or ketone functional groups. Zeaxanthin is a xanthophyll because it has hydroxy functional groups. Canthaxanthin is a 4-keto-carotenoid because it has a keto functional group at the 4' position of at least one end ring. Original.

made in the bodies of birds from basic biological precursors (amino acids) that are part of the diet of all birds.

The synthesis of melanin pigments requires not just adequate quantities of specific amino acids, but also a number of different metal ions (Ca, Zn, Cu, Fe). These minerals tend to be scarce in the diets of most birds and at the same time elevated levels of these elements can have detrimental effects on various body functions (reviewed in McGraw (2003)). It has been proposed that access to these metal ions might limit the capacity of some animals to synthesize melanin and hence be a primary constraint and basis for variation in expression of melanin (McGraw 2003). In this way melanin expression would be linked to diet quality. Alternatively, accumulating elevated levels of metals to increase melanin synthesis might negatively affect other body functions thus imposing a cost on melanin synthesis (McGraw 2003). Neither of these hypotheses has been experimentally tested.

Carotenoids are large, unsaturated lipid-soluble hydrocarbons that typically have two six-carbon rings connected by a chain of carbons. The simplest carotenoids, carotenes, contain only carbons and hydrogen atoms and are hydrophobic (Fig. 2.2). Xanthophylls have keto or hydroxy functional groups, which makes them less hydrophobic and can shift hues toward red (Fig. 2.2). Keto-carotenoids are a special group of xanthophylls with a keto functional group at the 4' position on one or both end rings. Keto-carotenoids are characterized by a red hue. Xanthophylls and keto-carotenoids are responsible for most yellow and red coloration in the feathers of birds.

In contrast to melanins, carotenoids cannot be synthesized by birds (or any vertebrates) from basic biological precursors (Goodwin 1984; McGraw 2006a). If they are used as integumentary colorants by birds, carotenoids must be

ingested as intact macromolecules and transported via the circulatory system to the site of pigmentation. Many species of birds with integumentary carotenoid displays can biochemically modify the pigments that they ingest (McGraw 2006a; Stradi 1998), but different species use different dietary precursors to produce different pigments used in feathers. Thus, only one or a few types of dietary carotenoids are useful as precursors for feather colorants for any given species (Hill 2002; McGraw 2006a). For instance, to obtain their red coloration, House finches (*Carpodacus mexicanus*) primarily convert orange dietary β -cryptoxanthin to red 3-hydroxy-echinenone (Inouye *et al.* 2001; Stradi *et al.* 1997; Stradi *et al.* 1996) whereas Northern cardinals (*Cardinalis cardinalis*) commonly convert yellow dietary lutein to red α -doradexanthin (McGraw *et al.* 2001a). Thus cardinals but not House finches will grow red feathers if maintained on a lutein-rich diet. Ultimately, all birds with carotenoid-based feather coloration must ingest specific dietary carotenoid pigments for expression of ornamental plumage display.

For considerations of genetic and environmental effects on color displays, it is useful to divide the process of pigmenting feathers with melanins or carotenoids into two phases: an acquisition phase and an utilization phase (Hill 1999; Fig. 2.3). Acquisition refers to the process of getting carotenoids pigments or the amino acid precursors for melanins from the environment into the gut. Utilization describes the process of absorbing, transporting, metabolizing, and depositing carotenoids or processing amino acids and synthesizing and depositing melanins (Fig. 2.3).

2.3 GENETIC AND ENVIRONMENTAL CONTROL

The degree to which genes or the environment determine expression of plumage coloration is central to the signal function of a color display. Honest signaling requires that ornamental traits be phenotypically plastic so that they can respond to environmental variation. It is this property of color displays—that they record the relative success that an individual has in dealing with specific environmental challenges—that makes them reliable signals of quality (Andersson 1994; Dale 2006; Hill 2006a; Kodric-Brown and Brown 1984). In contrast, arbitrary signals of attractiveness (Fisherian traits) evolve through a runaway process in which genes for choice for the trait become linked to genes for expression of the trait (Arnold 1983; Fisher 1958). Arbitrary signals must therefore be largely under genetic control and are not expected to be correlated with specific aspects of individual condition (Andersson 1994; Arnold 1983; Dale 2006). Signals of strategy are expected to be under strict genetic control with a polymodal distribution of expression such that each mode reflects a different, genetically determined reproductive strategy (Dale 2006; Dale *et al.* 2001). Therefore, before we can discuss the type of information signaled by pigmentation and the function of ornamental color displays, we have to consider the degree to which different plumage color traits are shaped by genes and the environment. If we find substantial environmental effects on

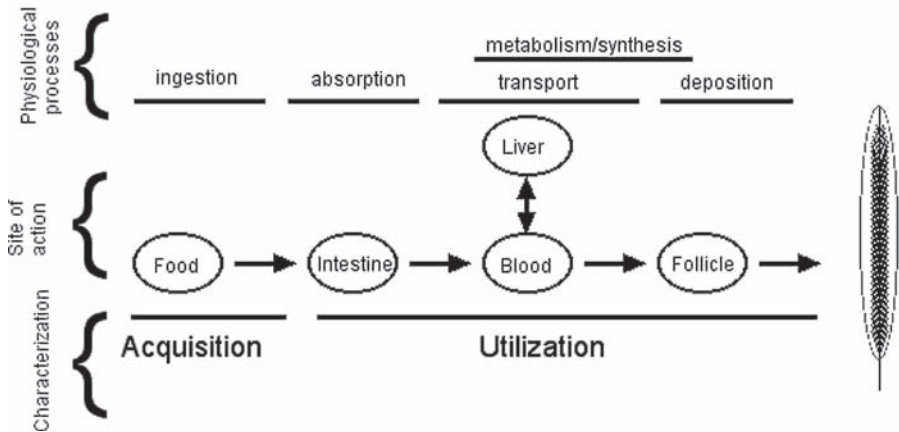


Fig. 2.3 A diagram of the pathway of carotenoid and melanin feather pigments from food to feathers. Acquisition refers to all processes related to getting pigments or pigment precursors into the gut. Utilization refers to those processes involved in getting ingested pigments or pigment precursors from food in the gut to functional pigments in feathers. Carotenoids must be ingested as macromolecules and then moved as in tact pigment molecules across the gut lining and to feathers. Carotenoids cannot be synthesized in the bodies of birds but they can be metabolically altered, potentially changing their color properties (e.g. from yellow to red). Melanin cannot be absorbed as macromolecules. The amino acids tyrosine, phenylalanine, and cysteine are melanin precursors derived from ingested protein, which are absorbed and transported to feather follicles. Within the follicle, amino acids are synthesized into melanin and deposited into feathers. Environmental variables have the potential to affect any step in these pigmentation processes. Original.

trait expression, we can then consider what specific environmental factors shape color expression and whether such environmental factors are related to individual condition.

2.3.1 Genetic Control of Color Traits

The basic, species-typical patterns of melanin and carotenoid coloration displayed by birds are clearly under genetic control (Buckley 1987). Regardless of the environment in which it is raised, a male House finch will always display a species-typical pattern of melanin and carotenoid pigmentation (Hill 1992, 1993). When canary breeders wanted to create a red Common canary (*Serinus canaria*), a species that has species-typical yellow coloration, they could not just change the environment in which birds were raised (Birkhead 2003). They had to capture a “red gene” (likely a gene coding for enzymes for conversion of yellow xanthophylls to red 4-keto-carotenoids) from another species of finch with species-typical red plumage—the Red siskin (*Carduelis cucullata*)—by crossing it with a canary (Birkhead 2003). Genes set the bounds for what color displays are possible in all avian species.

Because I am not considering species-recognition functions of coloration in this chapter, I will not further discuss the genetic architecture of species-typical coloration. Rather, in this chapter I focus on variation in expression within species-typical coloration. Such variation in expression can be in the form of discrete expression states—polymorphisms—or, more commonly, it can be in the form of continuous variation (Dale 2006). Variation can also take the form of different coloration (i.e. variation in hue, chroma, and brightness), which I will refer to as color quality, or it can be manifest as differing extent of color displays, which I will refer to as badge size (Fig. 2.4).

Expressions of polymorphisms are, without exception, under control of one or a few genes and are inherited as simple Mendelian traits (Lank 2002; Mundy 2006). The fundamental genetic control of carotenoid and melanin color morphs is clearly illustrated in the Gouldian finch (*Erythrura gouldiae*), a small estrildid finch that displays three discrete morphologies of cheek feather coloration—black, red, and yellow. The black plumage coloration is from eumelanin pigmentation, whereas red and yellow plumage colors are from carotenoid pigmentation (Brush 1968). Gross facial coloration is determined entirely by a sex-linked gene (Franklin and Dostine 2000); the environment in which a Gouldian finch is raised has no effect on what color morph it displays. The Gouldian finch is rather exceptional in having color morphs

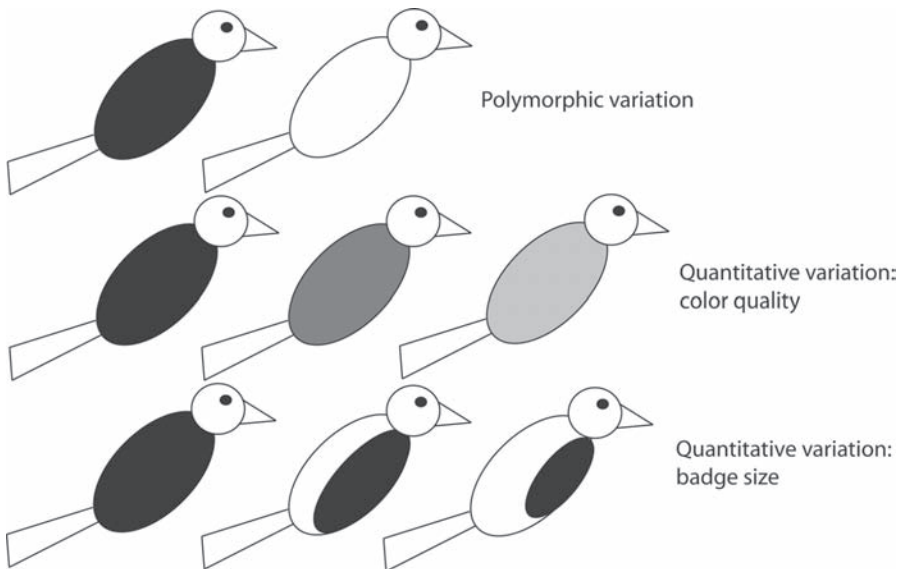


Fig. 2.4 Three types of variation in expression of plumage coloration. Color polymorphisms occur as two or just a few discrete expressions and are controlled through simple Mendelian inheritance. Quantitative variation is continuous over a range of expression and can affect the quality of coloration (e.g. hue, chroma, brightness) or the surface area with coloration (badge size). Quantitative variation arises from environmental effects and likely from the effects of numerous genes. Original.

involving both melanin and carotenoid coloration. Differences between morphs in most polymorphic species involve only relative amounts of melanin in plumage (Mundy 2006).

The number of genes involved in control of expression of color morphs will dictate the number of different plumage states than can be expressed. A good example of how the number of genes determines possible color expression is the control of melanin pigmentation by the melanocortin-1 receptor gene (*MC1R*). This gene determines expression of discrete dark/light morphs in at least four species of wild birds (Mundy 2006; Mundy *et al.* 2004). In species like the Bannaquit (*Coereba flaveola*), presence/absence of the *MC1R* gene at a single locus determines two discretely different morphs—black or yellow (Theron *et al.* 2001). However, *MC1R* also controls the relative darkness of plumage among Snow geese (*Chen caerulescens*), which show several intermediates between extreme dark and extreme light plumage. In Snow geese, three loci code for *MC1R* genes and the number of copies of *MC1R* is correlated with plumage type. If *MC1R* is expressed at no locus, a Snow goose will have snowy white breast plumage. As *MC1R* is expressed at more of the three loci, plumage gets darker. With only four different color types coded for (white and three degrees of dark) several plumage expressions are possible (Fig. 2.6).

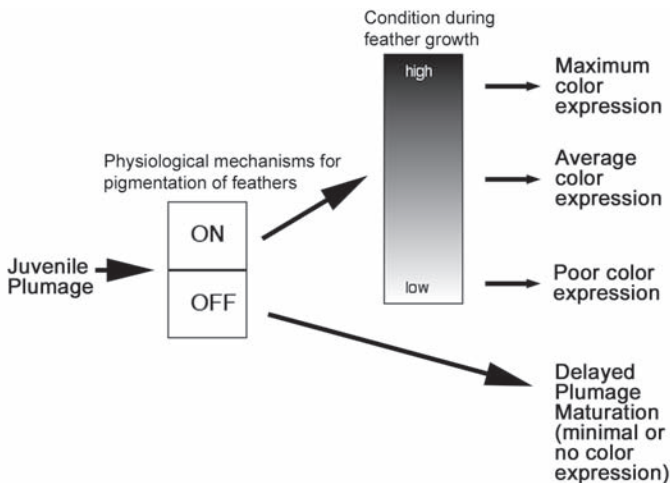


Fig. 2.5 Flow chart illustrating potential patterns of plumage development. Delayed plumage maturation describes an ontogenetic pattern whereby individual display subdefinitive (i.e. subadult) plumage coloration after they have reached sexual maturity. In males with delayed plumage maturation, mechanisms for producing definitive ornamental coloration are turned off. In the same way, in species with polymorphic color displays individuals turn on and off mechanisms for plumage coloration (e.g. light feathers or dark feathers). Within a morph, or a population of individuals in definitive plumage, individual variation is largely determined by environmental effects. Redrawn after Hill, G. E. 1996. *Auk* 113: 858-874, Fig. 1.

In many species of birds, there are age-specific plumage morphs (Rohwer *et al.* 1980). Such age-specific plumage displays do not represent an ontogenetic transition toward definitive plumage. Individuals in pre-definitive (hereafter subadult) plumages have reached adult morphology in all other respects and are sexually mature (Rohwer *et al.* 1980). The presence or absence of delayed plumage maturation within a population is under genetic control, but the specific expression of plumage coloration within an age group may be substantially influenced by the environment (Hill 1996) (Fig. 2.5). Subadult plumages appear to serve as signals of strategy (age and breeding status), and are presumably adaptations to competitive breeding contexts (Dale 2006; Senar 2006).

Variation in most color displays of most species of birds occurs not as discrete morphs but as continuous gradations. In other words, most melanin and carotenoid-based color displays are quantitative traits rather than Mendelian traits (Mundy 2006). We can think of such species having only one color morph with variation in expression within that morph. The effect of genes on expression of such quantitative color traits in wild birds is estimated by narrow-sense heritability of the trait, which is technically the proportion of total phenotypic variance that is due to additive genetic variance (the other two sources of variance being environmental and gene by environmental) (Falconer 1981).

Several studies have attempted to estimate the amount of variation that is due to genetic or environmental effects for continuously varying carotenoid and melanin ornaments in wild birds (reviewed in Mundy 2006). In all but two of these studies, however, the number of individuals included was less than 30 or there were no controls for rearing environment. In the two studies that avoided these basic design problems, researchers found substantial heritability of color displays. Roulin *et al.* (1998) used parent-offspring regression to look at heritability of the number of black eumelain spots in Barn owls (*Tyto alba*). They found that spot number had a high heritability, and they could find no significant effect of environment or gene-by-environment interactions on expression of spot number. In a study of the heritability of carotenoid-based bill coloration in Zebra finches (*Taeniopygia guttata*), additive genetic variance explained an estimated 34% to 73% of variance in expression of bill coloration, and the effects were not due to rearing environment (Price 1996; Price and Burley 1993). In this latter study, however, maternal effects including especially yolk carotenoids were not accounted for, and yolk carotenoids are known to affect adult bill coloration in Zebra finches (McGraw *et al.* 2005b). No comparable studies exist for heritability of carotenoid-based plumage coloration or melanin-based badge size, the two plumage pigment traits that have been subjected to the most study of environmental control and function.

The reason that there are so few convincing studies of the heritability of carotenoid and melanin coloration is that parsing morphological variation into genetic and environmental effects in studies of wild birds has proven

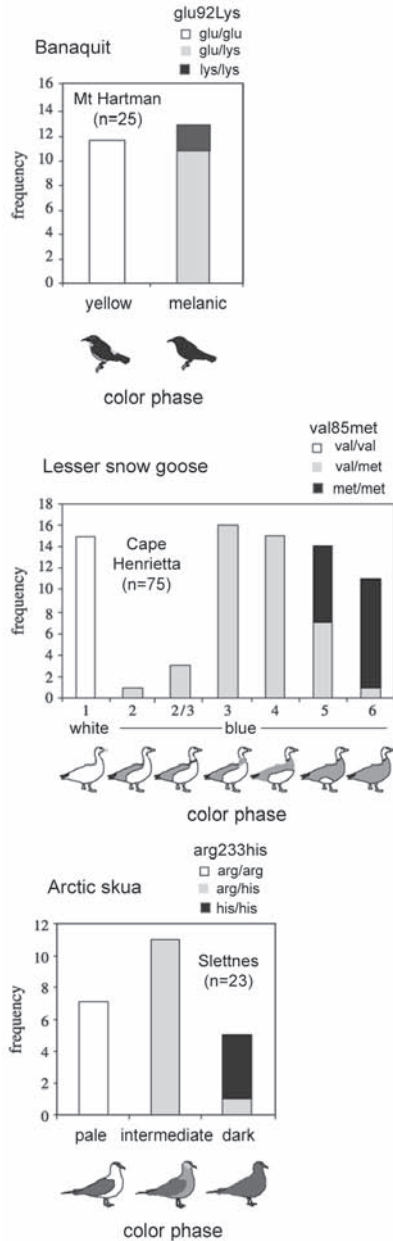


Fig. 2.6 Relationship between MC1R genotype and expression of melanin-based plumage coloration in three species of birds: (A) Bannanquite, (B) Snow goose, and (C) Parasitic jaeger. In all species, plumage darkness is proportional to number of copies of MC1R genes in an individual's genome. Redrawn after Mundy 2005. Proceedings of the Royal Society of London Series B 272: 1633–1640, Fig. 1.

extremely difficult. As will be reviewed in the next section, many color traits seem highly plastic and greatly modified by environmental conditions, which could lead to the conclusion that environmental effects are more important than genetic effects for most continuously varying color traits. However, demonstrating environmental effects on color displays does not mean that there are not also significant genetic effects on expression within a morph. Genetic and environmental effects on carotenoid and eumelanin-based plumage coloration are clearly in need of much more study.

2.3.2 Environmental Effects and the Information Content of Ornamental Coloration

The effects of environmental factors on expression of melanin and carotenoid plumage traits have been most effectively tested in common-garden experiments. In such experiments, groups of individuals are held under standardized conditions, and one or more environmental variables are manipulated. In the best studies, factors proposed to affect color display are manipulated at the time of molt, when new feathers are being produced, and all variables except the manipulated environmental factor or factors are held constant. Manipulating an environmental variable at a time offset from molt serves as a poor design to test for the direct effects of that variable on expression of plumage coloration.

Four external environmental conditions have been proposed to affect production of ornamental coloration in birds (Hill 2002, 2006a): pigment access, parasites, general nutrition, and social environment. I will consider the experimental evidence for the effects of each of these factors on carotenoid and melanin coloration. I will not review most correlational field studies, of which there are many and from which observations can be hard to interpret. Correlational field studies are reviewed in detail in Hill (2006a).

2.3.2.1 Pigment access

Pigment access concerns only carotenoid coloration. Melanin pigments are often ingested by birds, but dietary melanins are broken down into amino acid precursors before being absorbed in the gut. All melanin pigments used as colorants by birds have been built from amino acid precursors (McGraw 2006b).

In contrast, birds absorb and transport carotenoid pigments as intact macromolecules (McGraw 2006a). It has been known by aviculturists for millennia that captive birds will lose their red, orange, or yellow plumage coloration if kept on a diet deficient in red and yellow pigments (summarized in Hill (2006a)). Providing colorful foods to molting birds to promote bright red and yellow feather coloration, known as “color-feeding”, is an ancient art. Scientists were reporting color loss in captive birds with carotenoid-based coloration at least 30 years before carotenoid pigments were first described (e.g. Keeler (1893)).

The sensitivity of birds to carotenoid deprivation appears to vary substantially among species. Common canaries maintain carotenoid-based coloration when fed a diet of bird seeds (Völker 1938), but the same seed diet causes substantial loss of plumage coloration in House finches, American goldfinches (*Carduelis tristis*), and Northern cardinals (Hill 1992; McGraw *et al.* 2001a). Moreover, House finches, American goldfinches, and Northern cardinals show interesting differences in response to molting on seed diets that contain mostly lutein and zeaxanthin (McGraw *et al.* 2001a). House finches show a striking change in hue from red to yellow (Hill 1992; McGraw *et al.* 2001a), whereas cardinals show a less extreme change in hue from red to pink and goldfinches show little change in hue (Hill 1992; McGraw *et al.* 2001a). There are simple biochemical explanations for these different responses to a lutein-rich seed diet. House finches are unable to convert lutein to red pigments and so they grow yellow plumage with lutein deposited unaltered or used to make yellow metabolites like dehydrolutein and the canary xanthophylls (Inouye *et al.* 2001). In contrast, cardinals convert the lutein in seeds to the red pigment α -doradoxanthin, thus growing reddish plumage (McGraw *et al.* 2001a). American goldfinches fed lutein and zeaxanthin convert them into yellow canary xanthophyll a and b just as they would in the wild (McGraw *et al.* 2001a). Goldfinches still show loss of chroma (intensity) of coloration on this captive diet presumably because the amount of lutein and zeaxanthin in seeds is not sufficient to maximally pigment growing feathers. Thus, in captivity, birds must ingest enough of the right types of carotenoids to reach maximum color expression. The implications of these experiments are that conspecifics could get information about past success at foraging for scarce pigments by assessing carotenoid-based color displays (Endler 1983; Hill 1990).

A valid criticism of aviary experiments testing the effect of carotenoid access on expression of plumage coloration is that such experiments may not accurately represent the contribution of carotenoid access to the coloration of wild birds (Hudon 1994). The carotenoid content of the diets of wild birds have seldom been quantified, and in only one study of birds has carotenoid intake by individual adult birds been related to expression of ornamental plumage. In a wild population of House finches, carotenoid concentration in gut contents was significantly related to the hue of ornamental plumage being grown by males (Hill *et al.* 2002). This study both verified the potential importance of dietary carotenoids in wild birds (it had a significant effect) but also showed the potential for factors other than diet to affect color (carotenoids in diet explained only 5% (GEH unpublished data) of variation in color expression). Other studies that have implicated access to carotenoid pigments as a factor determining the coloration of wild birds have failed to provide a direct link between carotenoids in food and individual expression of plumage coloration (reviewed in Hill 2006a).

2.3.2.2 Parasites

The idea that parasites can depress expression of plumage coloration in birds dates to Wallace (1889) and was mentioned in passing by Fisher (1915).

However, it was not until Hamilton and Zuk (1982) published a model for host-parasite co-evolution with parasite resistance being signaled by color displays that the idea that parasites can affect expression of coloration in birds caught on with behavioral ecologists and field ornithologists. The basic idea is simple—parasites have detrimental effects on their host and their detrimental actions either directly or indirectly reduce the expression of ornamental coloration. An example of a direct effect of parasites is the inhibition of carotenoid uptake in the gut lining by intestinal coccidians (a protozoan parasite), thus leaving fewer pigments available for coloration (Allen 1992; Ruff *et al.* 1974). Parasites could also have indirect effects on color displays by causing a reallocation of energy or resources away from mechanisms of feather color to defense against the parasites. Despite the widespread acceptance of the idea that parasites can depress expression of ornamental coloration, relatively few experimental tests have been conducted on the effects of parasites on expression of melanin and carotenoid coloration.

Studies with House finches and American goldfinches have used experimental infections to simultaneously test the effects of coccidiosis on melanin and carotenoid plumage coloration in the same birds. For each species, one group of males was kept free of coccidia, whereas a second group was either inoculated with coccidial oocysts (House finches) or simply not treated for coccidiosis and allowed to develop an infection (goldfinches). The results of both studies were the same—coccidiosis had a significant negative effect on expression of carotenoid-based but not melanin-based coloration (Hill and Brawnner 1998; Brawnner *et al.* 2000; McGraw and Hill 2000). In the House finch study, the melanin coloration that was assessed was non-ornamental tail coloration, but in the goldfinch study expression of ornamental black caps was assessed. Neither the size nor the saturation or brightness of the black coloration of caps was different between the parasitized and non-parasitized male goldfinches (McGraw and Hill 2000).

Other infection studies with male House finches showed that mycoplasmosis, a bacterial infection, also depresses ornamental carotenoid coloration of the breast but not melanin coloration of the tail (Hill and Brawnner 1998; Hill *et al.* 2004). These latter studies with *Mycoplasma gallicepticum* are important because previous experimental studies had all been conducted with coccidia, an intestinal parasite that is known to directly inhibit the uptake and perhaps the transport of carotenoids (Brawnner *et al.* 2000). Differential effects on carotenoid versus melanin ornaments might be explained by a gut parasite like coccidia having a direct and disproportionate effect on carotenoid coloration. Other, non-intestinal diseases might more equally affect melanin and carotenoid ornaments. Mycoplasmosis, however, is an upper respiratory infection in finches that should not directly target carotenoid pigmentation. The fact that such a systemic, non-intestinal infection affected carotenoid ornaments but not melanin pigmentation provides evidence that carotenoid and melanin coloration have different sensitivities to parasite infection in general, at least in cardueline finches. More infection experiments on a more taxonomically diverse set of species are

needed before we will know how far these studies with cardueline finches can be extrapolated.

No direct experimental tests of the effects of parasites on plumage have been conducted in the field, but many correlative field studies of color and parasites have been conducted (reviewed in Hill (2006a)). The study that comes closest to a field manipulation of parasites during molt was a study of a wild population of House finches by Thompson *et al.* (1997). They captured males and ranked both carotenoid-based feather coloration and the degree of infection by avian pox and feather mites. They found significant relationships between plumage redness ranks and ranks for both pox and mite infection. Most intriguing, they recaptured a subset of these males after fall molt and compared change in plumage hue to the level of parasite infection at first capture (going into molt). They found a significant relationship between degree of pox and mite infection and decrease in coloration between sampling periods. These observations suggest a causal link between carotenoid-based plumage coloration and parasite load in this wild population of House Finches.

In the only experimental field study of the effects of parasites on melanin coloration, Fitze and Richner (2002) experimentally infected the nests of some Great tit (*Parus major*) pairs with hen fleas (*Ceratophyllus gallinae*) while removing the fleas from the nests of other pairs. They found that fleas had a significant negative effect on the width of the black breast stripe grown in the subsequent molt but no effect on the carotenoid-based yellow coloration or on the color quality of the black bibs grown later. In this tit experiment, unlike the experiments with Goldfinches and House finches reviewed above, the manipulation of parasites occurred months before ornamental feathers were grown, and parasite levels were presumably not different at the time of molt. So this study is not evidence for direct effect of parasites on production of eumelanin coloration.

From these few experimental studies of the effect of parasites on pigmentary coloration, we can tentatively conclude that the quality of carotenoid pigmentation encodes information about previous exposure to parasites, but that melanin pigmentation, including both patch size and color quality, is generally less sensitive to the direct effects of parasites. These conclusions regarding the effects of parasites on pigmentary coloration are based on a handful of experimental studies conducted on species in one subfamily of songbirds (carduline finches) and much more investigation is clearly needed.

2.3.2.3 Nutrition

General nutrition (and for this discussion I am excluding intake of carotenoid pigments as part of general nutrition) has the potential to affect plumage coloration in two ways. First, nutrition may affect access to the basic biological precursors needed to synthesize melanin pigments and hence constrain the amount of melanin available for ornamental coloration (i.e. affect acquisition of amino acids or minerals; Fig. 2.3). Second, nutrition might affect biological

systems needed to synthesize, modify, absorb, transport, or deposit melanin or carotenoid pigments (i.e., affect utilization; Fig. 2.3). A few experimental studies have tested the effects of nutrition on expression of melanin and carotenoid pigments. Correlative studies are reviewed in Hill (2006a).

A study of House finches looked at the effect of food deprivation simultaneously on expression of non-ornamental melanin coloration of tail feathers and ornamental carotenoid-based breast feather coloration. Modest food deprivation had a significant effect on expression of carotenoid-based ornamental coloration, regardless of whether birds were provided with yellow precursors to red feather pigments or red feather pigments directly (Hill 2000). In contrast, nutritional deprivation has no effect on melanin tail pigmentation (Hill 2000). This study suggests that melanin-based and carotenoid-based plumage coloration may have different sensitivities to nutritional restriction, but it is possible that the response would have been different if the melanin coloration under study had been ornamental.

In a study of the effect of food deprivation on expression of ornamental carotenoid pigmentation in American goldfinches, McGraw *et al.* (2005a) found that the same modest food deprivation that caused reduction in coloration in House finches also caused loss of coloration in goldfinches. Furthermore, by looking at carotenoid concentrations in the tissues of goldfinches, they concluded that the effect of deprivation manifest at pigment assimilation into circulation, not at pigment metabolism or deposition (McGraw *et al.* 2005a). The conclusion that food deprivation affects carotenoid assimilation and not carotenoid metabolism is consistent with the observation in House finches that food deprivation affects feather coloration regardless of whether precursors or red pigments are provided (Hill 2000).

The effects of nutrition on the size and achromatic brightness of ornamental patches of melanin-based plumage coloration have been studied primarily in the House sparrow (*Passer domesticus*), a species with a large black bib that is pigmented with eumelanin (Fig. 2.1A). In an experimental study of the effects of food deprivation on plumage coloration, McGraw *et al.* (2002) found no effect of food access on the size or coloration of the badges of male House sparrows. Restricted food access during molt also failed to affect the brown coloration of Brown-headed cowbirds, *Molothrus ater* (which is partly pigmented by eumelanins and partly by phaeomelanins), but the same manipulation did affect the hue and chroma of the iridescent coloration of cowbirds (McGraw *et al.* 2002). In another experimental aviary study, Gonzalez *et al.* (1999) found no significant effect of protein content of diet on the size or brightness of male badges. And finally, in the most carefully controlled study to date, in which the amount of melanin precursors (phenylalanine and tyrosine) in the diet was experimentally manipulated in flocks of captive male House sparrows, Poston *et al.* (2005) found no effect of access to melanin precursors on the size of the black bibs of males, but males on diets with restricted phenylalanine and tyrosine grew lighter (less black) bibs.

These few studies suggest that, independent of intake of carotenoid pigments, overall nutrition can affect expression of carotenoid coloration. In contrast, the size of melanin patches in plumage seems to be comparatively less sensitive to nutrition. The achromatic brightness of melanin patches may be affected by ingestion of specific amino acids, but this effect seems to be manifest only when amino acid composition of foods is manipulated to extreme levels. More studies of the effects of diet on carotenoid and melanin pigmentation in a wider range of taxa are needed.

2.3.2.4 Social status and color

In the extensive literature on status signaling related the plumage pigmentation (reviewed in Senar 2006), the focus is on how color displays might affect the dominance status of a bird. The reverse consideration—how dominance status might affect production of ornamental coloration—is key to understanding the signal content of at least some color displays. The effect of social environment on production of ornamental feather coloration has been tested in only one experimental study. McGraw *et al.* (2003) monitored the social status of male House sparrows during molt and recorded the pre- and post-molt badge sizes of the males. Males that were subordinate grew smaller badges than birds that were dominant, and badge size before experimental treatment did not predict badge size after treatment. This study suggests that social status during molt might significantly affect expression of eumelanin pigmentation. No equivalent study has yet been conducted on a bird species with carotenoid ornamentation. Experimental studies focused on the size but not color of fleshy comb in Red junglefowl (*Gallus gallus*) also have shown that changes in dominance status results in a change in ornament expression (Parker *et al.* 2002).

2.3.3 The Information Content of Pigment-based Color Signals

2.3.3.1 Morphs

Dale (2006) proposed that color displays that function as signals of strategy should show a polymodal distribution and be under tight genetic control. As just reviewed, polymorphic color displays fit these requirements for signals of strategy. In the Ruff (*Philomachus pugnax*), for instance, the primary color morphs, dark or white, are determined by sex-linked genes with negligible environmental effects (Lank *et al.* 1995). These dark/light color morphs perfectly predict the reproductive tactics of males. White males are non-aggressive satellites around leks, whereas dark birds are aggressive displayers on the leks. Strategy is honestly signaled by color morph, and the system is stable because both displaying males and satellite males obtain reproductive success through their honestly signaled strategies (Lank *et al.* 1995). Because plumage polymorphisms are Mendelian traits, they are, by definition, not condition dependent, and hence are poor candidates for indicators of individual quality.

Most polymorphic variation in color displays involves only melanin pigmentation. In a few species of birds (e.g. Gouldian finch) morphs involve both carotenoid and melanin pigmentation. Why the great majority (perhaps 99%) of such polymorphic signals of strategy are based on melanin rather than carotenoid pigmentation remains unexplained. The propensity for strategy signals to be based on melanin rather than carotenoids may result from the greater environmental sensitivity of carotenoid-based color displays, which would make such displays more ambiguous markers of strategy than melanin displays.

2.3.3.2 Continuous variation in color display

The studies just reviewed show that carotenoid and melanin-based color displays have a substantial environmental component and hence are condition dependent. Both melanin and carotenoid-based ornaments, therefore, have the potential to serve as reliable indicators of individual quality, honestly signaling how well an individual has dealt with various environmental challenges. However, the aspects of condition signaled by melanin and carotenoid pigments appear to be distinct.

Variation in expression of carotenoid ornamentation among males in populations of songbirds appears to be affected by carotenoid access, parasites, and general nutrition. Carotenoid access and general nutrition might be tightly correlated if carotenoids are ingested passively so that increased food intake invariably leads to increased carotenoid intake. However, it has been suggested that foods rich in carotenoids are not necessarily the foods richest in proteins or other nutrients needed to grow strong feathers and maintain body systems (Hill 2002). If this is the case then birds may have to forage separately for carotenoid-rich foods and foods that are otherwise nutritious. Such specialized foraging would make it particularly difficult to attain maximum carotenoid display and would make carotenoid pigmentation a particularly sensitive indicator of foraging ability and a particularly useful signal for females who needed to assess male foraging ability. Experimental studies also indicate that nutrition, independent of carotenoid access, can affect expression of carotenoid coloration. Such a nutritional effect on coloration may simply reinforce the link between foraging and carotenoid displays that results from the need to ingest carotenoid pigments or it may produce effects on carotenoid coloration that are distinct from the effects caused by pigment access (see below). Because carotenoid pigmentation is affected a variety of parasites, females could also potentially use carotenoid coloration to assess the overall health state of a male during the previous molt period. Thus, carotenoid pigmentation seems to be a reliable signal of health state and foraging ability.

In contrast to results of studies of carotenoid coloration, experimental studies conducted to date have generally not found direct effects of nutrition or parasites on expression of melanin coloration. The observation that the sizes of eumelanin badges are insensitive to nutritional condition fits well with the conventional wisdom of zookeepers and aviculturists that it is

difficult to maintain carotenoid coloration in captive birds (primarily because captive diets are deficient in carotenoid pigments but possibly also because of the overall nutrition of captive diets is sometimes poor) but that any diet that keeps a bird alive will maintain melanin displays. From the data at hand, it seems that females would gain little information about a male's history of infection or success at foraging by assessing the size of melanin-based badges.

Expression of black eumelanin pigmentation is well known to correlate with the social status of individuals (Senar 2006), and social status appears to be the primary information signaled by the size of eumelanin badges. There are two likely manners that correlations between badge size and social dominance might arise. First, constraints might determine both the social status of an individual and its ornamentation, thus creating a correlation. Alternatively, individuals might adjust their ornament display in anticipation of future status, likely through endocrinological control mechanisms (Kimball 2006). In other words, social status might directly determine expression of ornamental coloration. One recent study showed that the social status of individuals during molt can affect the size of badges that are grown (McGraw *et al.* 2003), and this study suggests that birds might adjust the size of melanin badges in anticipation of future status. The well known relationship between the size of eumelanin patches and social status suggest that receivers might gain reliable information about the social status and resource-holding potential of an individual by assessing eumelanin badge size. With the limited data at hand it appears that social status during molt is the primary environmental factor that determines expression of eumelanin coloration and hence that social status is the primary signal conveyed by melanin badge size, but more experimental studies are needed.

2.3.3.3 Degree of detail in single and multiple pigment signals

One interesting question is whether a single patch of ornamental coloration can record complex information about how an individual has dealt with different environmental challenges (Wedekind *et al.* 1998). For instance, do carotenoid access, general nutrition, and parasites leave unique signatures on carotenoid color displays? In general, one would expect the answer to be "no". Coloration does not have sufficient dimensionality to encode a detailed record of individual condition. Females will know that a male with maximally expressed carotenoid coloration has done well in acquiring pigments, gaining access to nutrition, and avoiding parasites, and that males with reduced carotenoid display will have done less well in meeting one or more of these challenges. Specific decoding of information is not necessary for assessment of the signal to be of value to the female.

There are ways, however, in which some details of male condition might be conveyed by carotenoid signals. As a general rule, the concentration of a given type of carotenoid pigment that is deposited in feathers will determine the chroma of the color display, whereas the mix of pigments, and particularly the proportion of yellow xanthophylls and red keto-carotenoids, will deter-

mine hue (Inouye *et al.* 2001; Saks *et al.* 2003; Andersson and Prager 2006). Thus, different environmental effects might be discernable if one environmental factor had its effect primarily on pigment concentration, whereas another had its effect primarily on pigment composition. Wedekind *et al.* (1998) went even further and proposed that ratios of specific types of carotenoid pigments (as opposed to ratio of different classes of molecules as in yellow xanthophylls and red keto-carotenoids) could give females information about male attributes like immunocompetence. They argued that if some types of carotenoids are more valuable as immunoenhancers and hence tied more closely to immune function than other types of carotenoids then the ratio of these pigments could reveal disease state or immunocompetence. This requires an ability by females to perceive ratios of specific pigments (rather than classes of pigments). Such specific decoding of a carotenoid signal has yet to be demonstrated in any species.

While we generally expect nutrition and pigment access to have similar effects on carotenoid display, there is at least one mechanism for general nutrition and carotenoid access to have distinct and at least partially independent effects. Shawkey and Hill (2005) recently showed that carotenoid pigments produce color displays by absorbing light of specific wavelengths from the white light reflected from underlying structural coloration. Some aspects of “carotenoid pigmentation”—particularly brightness and perhaps UV chroma—are therefore more a function of the quality of white light reflected by underlying structures than they are a function of absorption of light by carotenoids (Andersson and Prager 2006; Shawkey and Hill 2005). An intriguing but untested idea is that nutrition may affect properties of the white structural coloration (as has recently been shown for blue structural coloration; McGraw *et al.* (2002); Siefferman and Hill (2005)) without affecting pigment concentration or composition. In this way some aspects of carotenoid coloration such as brightness and UV chroma might be affected by diet, whereas pigment acquisition might affect hue and yellow chroma. This idea remains to be tested.

Badyaev *et al.* (2001) similarly proposed that different aspects of red carotenoid coloration in male House finches—specifically pigment quality, pigment symmetry, patch size, and patch symmetry—might each have a different sensitivity to environmental perturbations and hence might each signal something different about an individual. That females could get specific information about how prospective mates handle specific environmental challenges from different components of a single color display is an intriguing idea and deserves more study.

Many species of birds have both carotenoid-based and melanin-based coloration, and the function of such multiple ornaments is a topic of current interest among evolutionary biologists (van Doorn and Weissing 2004). One hypothesis put forth to explain multiple signals is that they each ornament signals the same aspects of individual quality, providing a redundant signal to females (Møller and Pomiankowski 1993). This redundant-signal

hypothesis seems not to hold with respect to carotenoid and melanin coloration because each type of pigment display has a distinct environmental sensitivity and hence each will contain different information about an individual. An alternative hypothesis is the multiple messenger hypothesis, which proposes that each ornament conveys different information to the receiver (Møller and Pomiankowski 1993; van Doorn and Weissing 2004). Evidence to date suggests that pigment quality of carotenoid ornaments conveys information about foraging ability and parasite history to females, whereas badge size of melanin ornaments conveys information about social status and resource holding potential. Thus, display of both melanin and carotenoid coloration seems best explained by the multiple message hypothesis.

2.4 THE FUNCTION OF CAROTENOID AND MELANIN COLORATION

As reviewed above, evidence suggests that both carotenoid and melanin plumage colors are condition-dependent traits that encode specific information about the quality of the bearer. Correlations between trait expression and components of individual condition only become interesting in the context of conspecific signaling, however, if expression of the trait is assessed by conspecifics, if conspecifics respond to the trait, and if conspecifics gain through their assessment and response. Carotenoid and melanin coloration have been proposed to function as signals of quality and to be used by receivers in two ways: assessment of potential mates and appraisal of potential competitors. Evidence for each of these functions of coloration has been reviewed recently in detail (Hill 2006b; Senar 2006), and I will not repeat those reviews here. Rather, I will provide an overall assessment of current evidence for ornament function and then focus on whether there is evidence for a payoff for assessment of carotenoid and melanin coloration.

In previous publications, my collaborators and I have suggested that because carotenoids seem more sensitive to pigment access, general nutrition, and parasites than do melanin ornaments, carotenoid ornaments should be more commonly used in mate choice than melanin ornaments (Hill and Brawner 1998; Badyaev and Hill 2000; McGraw and Hill 2000). Furthermore, we have suggested that because melanin pigmentation seems to reflect and be shaped by social status more than are carotenoid pigments, melanin ornaments should function more commonly as signals in intrasexual aggressive interactions than carotenoid pigments (Badyaev and Hill 2000; McGraw *et al.* 2002, 2003).

These suggestions are laden with assumptions that have not been adequately addressed in the literature. Importantly, these ideas assume that females should be more interested in parasite resistance and foraging ability than social status when choosing a mate. It is not hard to envision, however, many circumstances in which social status might be more important than

parasite resistance or foraging ability in determining the quality of a mate from the perspective of a female. Perhaps not surprisingly, emerging empirical data on the role of carotenoids and melanins in female mate choice indicate that melanin-based and carotenoid-based ornaments both commonly function in female mate choice (Hill 2006b). Based on the nearly 20 studies of carotenoid-based plumage pigmentation and nearly 30 studies of eumelanin-based plumage coloration, there is no basis for stating that either carotenoids or eumelanins are used more commonly as criteria in female choice (Hill 2006b).

The conclusion that the size of eumelanin-based badges more commonly serve as a signal of resource holding potential than does the color quality of carotenoid ornaments, on the other hand, seems generally consistent with empirical studies (Senar 2006). With two exceptions, all of the many experimental demonstrations of color displays serving as signals of social status concern the badge size of eumelanin ornamentation (Senar 2006). Moreover, several experimental studies have failed to find evidence that carotenoid-based coloration serves as a signal of social status.

My working premise for the remainder of this chapter will be that expression of both carotenoid and melanin coloration is assessed by conspecifics—melanin in both mate choice and dominance assessment and carotenoids primarily in mate choice. Thus in birds we have assessment of condition-dependent expression of pigment-based color displays. We are left with one fundamental question: do individuals benefit by assessing the pigment-based color displays of conspecifics?

2.5 BENEFITS TO ASSESSMENT OF PIGMENT DISPLAYS

2.5.1 Mate Choice

With regard to female mate choice, there are two primary means by which females could benefit from assessment of the pigment displays of potential mates (Andersson 1994). First, by choosing the most ornamented males, females could receive “direct” benefits, such food for themselves or food for their offspring, if ornament expression was correlated with the provisioning rates of males. Alternatively, females could gain “indirect” genetic benefits for offspring if expression of melanin and carotenoid was correlated with the genetic quality of males. I will consider the evidence that by choosing mates based on carotenoid or melanin pigmentation females gain direct or indirect fitness benefits.

2.5.1.1 Direct benefits

In species with biparental care, which includes most species of birds (Ligon 1999), food resources are the most obvious benefits that females stand to gain by choosing a mate based on expression of plumage coloration. Males can provide food to the female prior to egg laying or during incubation, or they can bring food to offspring. Female might benefit to different degrees from food

received under these different conditions, and there are complications in trying to quantify food resources provided directly to females versus food provided to offspring, as will be discussed below.

Only one study has looked at male feather pigmentation in relation to provisioning of females. In the House finch, males with brighter carotenoid coloration provided more food to incubating females (Hill 1991). Because female choice for males with redder and more saturated carotenoid coloration is well established, this study of incubation provisioning is among the clearest demonstrations of a direct benefit to females linked to assessment of a pigment display.

Most studies addressing resource benefits related to feather pigmentation have looked at the rate at which males provision young in nests. In House finches (Nolan and Hill, in prep) and in two populations of Northern cardinals (Linville *et al.* 1998; Jawor *et al.* 2004; Jawor and Breitwisch 2004) there was a significant positive relationship between the hue and intensity of carotenoid-based breast feather coloration and rate at which males provisioned young. These studies support the idea the females gain direct resource benefits by assessing carotenoid-based coloration. However, in the Linnet (*Carduelis cannabina*) (Drachmann 1998), Yellowhammer (*Emberiza citrinella*) (Sundberg and Larsson 1994), and Zebra finch (Burley 1988) males with brighter carotenoid-based coloration provided less food to offspring males with drabber displays. Furthermore, Jawor and Brietswitch (2004) found no relationship between the carotenoid-based plumage coloration of female cardinals and provisioning rate, but provisioning rate was significantly positively related to carotenoid-based bill coloration among females.

Extent of black eumelanin pigmentation of males has been found to be positively correlated with provisioning of nestlings in Barn owls (Roulin *et al.* 2001), House sparrows (Møller 1988; Voltura *et al.* 2002), Medium ground finches (*Geospiza fortis*) (Price 1984), and in one study of Pied flycatcher (*Ficedula hypoleuca*) (Saetre *et al.* 1995). But in other studies of the Pied flycatcher, nestling provisioning did not relate to the amount of black pigmentation in the plumage of males (Saetre *et al.* 1997; Dale *et al.* 1999; Rinden *et al.* 2000). In Great tits, males with more black in their breast plumage defended nests more (Norris 1990), another form of male investment.

All and all it is hard to draw general conclusions from these studies of resource investment in relation to either carotenoid or melanin plumage coloration. Given that experimental studies show that carotenoid plumage coloration is sensitive to aspects of foraging—nutrition and pigment acquisition—during molt whereas melanin plumage coloration is generally not affected by these environmental factors, I speculate that relationships between provisioning and pigment coloration arise by different mechanisms in carotenoid and melanin ornaments. Males with brighter carotenoid coloration likely provide more food to offspring because their foraging skills permit them to acquire more food during breeding. In contrast, the size of

eumelanin patches seems to most often function as a reliable indicator of social status and resource holding potential during molt, and it is likely that male with large melanin badges provide more food during molt because they monopolize better resources.

Consistent with these ideas, studies of the House finch have linked foraging during molt to male plumage coloration and then male plumage coloration to provisioning of females and offspring (Hill 2002). In House sparrows, in contrast, nutrition during molt does not affect badge size, but still males with large badges tend to feed nestlings more (Møller 1988; Voltura *et al.* 2002). Badge size in House sparrows is related to the quality of resources defended (Møller 1988; Veiga 1993), so it seems likely that badge size is linked to provisioning not because large-badged males are better foragers but because large-badged males have greater ability to hold resources. From the perspective of the female, however, the mechanism by which color signals are linked to resource investment may not matter.

Nearly as many studies have failed to find relationships or have found negative relationships between pigment coloration and resource benefits as have found positive relationships. However, all but one of these studies concern nestling provisioning, and as Griffith and Pryke (2006) argue, rates of nestling provisioning in relation to ornamental coloration are confounded by the fact that, in all species studied, females also provide food. This means that there is both an absolute feeding rate by males and a feeding rate that is relative to the resources provided by females. Under some conditions, females are expected to provide more food to the offspring of highly ornamented males (Burley 1988), which might cause highly ornamented males to feed less. Moreover, in territorial species, ornamented males may control areas with better food resources, and in such cases males may contribute resources to offspring through defense of resources rather than direct provisioning. Thus, a finding that there is no relationship with ornamental coloration and male provisioning or even a negative relationship between provisioning and ornamentation, does not mean that females fail to receive resource benefits through their choice of mates.

To circumvent these complications with quantifying male resource allocation, future studies should focus on forms of male allocation that are not confounded by female allocation, such as provisioning of the female. In addition, experiments that disentangle resource allocation to nestlings by males and females, such as by removing the female for a period of time and observing male allocation, will better test the idea that male ornamentation is a signal of resource investment. Finally, to better understand how male ornamentation is linked to the acquisition of food by a female and her offspring, experiments should be designed to distinguish male resource defense from male foraging efficiency. Currently, after a decade of work, we are left with little direct evidence for resource benefits accruing to female birds who chose males with more elaborate ornamental feather pigmentation.

2.5.1.2 Good genes

If males in a population vary in the fitness of their genotypes and if genetic quality is correlated with expression of melanin- or carotenoid-based plumage coloration, then females could receive genetic benefits for their offspring by mating with well ornamented males. To date the best evidence for good genes associated with ornament expression in birds has been for morphological features of tails (Møller 1990; Petrie 1994). Evidence for good genes related to melanin or carotenoid feather coloration is indirect.

Genes for resistance to parasites have been the focus of studies of good genes related to plumage coloration. How individuals resist the effects of pathogens can have a large effect on their fitness, and females should benefit if they can identify males with better-than-average genes for parasite resistance that can be passed on to offspring. As I presented earlier in this chapter, studies of parasites and color displays have primarily focused on how parasites affect the production of plumage coloration, and it was found that production of carotenoid but not melanin displays are sensitive to parasites. Thus, history of infection may be recorded in carotenoid-based plumage displays. If all birds are exposed to the pathogen, then plumage coloration may be a signal of disease resistance and not simply a record of history of exposure. Disease resistance may, in turn, have a heritable component, in which case color could correlate with genetic quality. However, the demonstrations of effects of parasites on plumage coloration are several important steps removed from demonstrating good genes related to color display.

One key prediction of good genes models related to plumage coloration is that plumage coloration of males predicts the ability of males to withstand the effects of a pathogen. In a study of Eurasian greenfinches (*Carduelis chloris*), Lindström and Lundström (2000) infected males with a virus and looked at time to infection and clearance related to carotenoid-based yellow plumage coloration. Ability to resistance and clear infection was positively related to carotenoid display. Similarly, my lab group experimentally infected male House finches with a bacterial pathogen and found that redder males were better able to clear infection (Hill and Farmer 2004). Horak *et al.* (2001) looked at plumage coloration of male Eurasian greenfinches in relation to immune responsiveness, which they argued was a good proxy for ability to clear disease, and found that brighter males showed better immune responsiveness. All of these studies provide only indirect evidence for good genes related to feather coloration because in all cases, males with brighter coloration could be in better phenotypic condition and their better condition may make them better able to resist infection. Good genes need not be invoked, but they remain a possible explanation for some of the effects seen in these studies.

Despite great interest in the topic, these are the best studies to date for good genes benefits related to mating with males with elaborate melanin or carotenoid plumage color displays. In recent years, great technological

advances have been made in the ability to genotype organisms and uncover the function of genes. Such techniques have yet to impact studies of good genes related to sexual selection, but this will change profoundly within the next few years. As we reach the point where we can quantify the fitness of different genotypes in different environments (e.g. under exposure to different pathogens; Wang *et al.* 2005), we can directly assess the association of plumage color displays with the most fit genotypes. Such studies will provide a direct test of good genes models.

2.5.1.3 Reproductive success

If well-pigmented males provide more resources or good genes, one would expect such male attributes to have a positive effect on female fitness. However, it has proven difficult enough to convincingly test the idea that male plumage coloration predicts the amount of resources or the quality of genes that a female receives from that male. Demonstrating that females get an actual fitness payoff from their choice of highly ornamented males has yet to be convincingly demonstrated in any wild species. In several studies, researchers have looked for correlations between male coloration and the reproductive success of pairs, but such relationships could arise in a number of ways. Thus, even the few demonstrations of higher reproductive success for females paired to more ornamented males provides only indirect evidence for a fitness payoff for choice based on male plumage pigmentation.

Attempts to link reproductive success of females to the carotenoid or melanin pigmentation of their mates have yielded mixed results. The number of young fledged by pairs of House finches per year (McGraw *et al.* 2001b) was significantly positively related the hue of the carotenoid-based plumage coloration of males. However, there was no significant positive correlation between carotenoid coloration and annual reproductive success in field studies of Northern cardinals (Jawor and Breitwisch 2004) or Yellowhammers (Sundberg 1995). More studies have looked at eumelanin coloration and reproductive success. In House sparrows, Jensen *et al.* (2004) found the size of the eumelanin badges of males was positively correlated with not just annual but lifetime reproductive success. Pairing with such males would presumably be a benefit to females, but this was not considered in the study. In Medium ground finches males with more black in their plumage fledged heavier offspring (Price 1984). The spottiness of male Barn owls was significantly correlated with annual reproductive success (Roulin 2001). In Black-capped chickadees (*Poecile atricapilla*) the UV-chroma rather than size of eumelanin badges predicted annual reproductive success (Doucet *et al.* 2005).

These studies hint at fitness benefits for females that pair with males with more elaborate carotenoid or melanin plumage coloration. All of these studies are correlative, however, and it is quite possible that the relationship between male pigmentation and the reproductive success of pairs has nothing to do with the good genes or resources contributed by males. For instance, higher quality females would be expected to pair with more attractive males and

higher quality females may produce more young than lower quality females regardless of the contribution of their mates. To demonstrate definitively that females receive direct fitness benefits through their choice of mates, a series of experiments will be needed that uncouple the effects of color quality and badge size per se from the effects of provisioning. For instance, if the badge size of males was manipulated (and assuming that males retained their original provisioning rates), then the effects of badge size (e.g. attracting high quality mates) and the effects of provisioning could be assessed independently.

2.5.2 Status Signaling and Receiver Benefits

As I have worked through this chapter I have moved from topics for which there is solid experimental evidence for conclusions (e.g. the environmental effects on pigmentation and the function of pigment displays), to topics with limited empirical testing (fitness benefits of mate choice for pigment displays), and I now end with a topic for which there is virtually no data. Status signaling has been the focus of numerous studies over the last few decades, and it is firmly established the pigment displays, and particularly melanin-based badge sizes, can be reliable signals of male dominance status (reviewed in Senar (2006)). In every empirical study to date that has considered benefits of honestly signaling status via plumage coloration, however, it is the costs or benefits to signaler rather than the receiver that has been the focus of study. No empirical study has attempted to measure the fitness benefits of assessing fighting ability through color display.

The reasons for the lack of empirical studies directed at measuring the benefits of assessing the pigment displays of rivals is simple. Such studies are very difficult to perform. Ideally one would compare the outcome of interactions in which a signal is assessed versus the outcome of interactions when the signal is not assessed. Establishing a group of individuals that fail to assess signals but are in every other respect the same as a group that assesses signals is not likely to be possible in any population of birds. Alternatively, an investigator could remove the status signal, as has been done in numerous experiments focusing on the consequences for the signaler, and focus on the fitness consequences of the receiver. Such studies are needed if we are to understand the benefits of assessing a pigment signal in the context of intrasexual aggression.

2.6 CHAPTER SUMMARY

Over the last two decades, great strides have been made in our understanding of how ornamental feather pigmentation can function as a signal. For at least a few species of birds, we now have a detailed information on the specific pigments that create both melanin and carotenoids displays. We have a reasonable understanding of the genetic and environmental effects on production of both polymorphic and continuously varying coloration.

Expression of polymorphic color traits is, without exception, controlled by a simple Mendelian mode of inheritance and these signals seem generally to function as signals of strategy. No studies have shown that such polymorphic pigment displays function as signals of quality or attractiveness, and theory suggests that they are poor candidates for such signaling. Continuously varying or quantitative melanin and carotenoid pigmentation, in contrast, meets the theoretical requirements for signals of quality. Experiments with a few species of passerine birds indicate that production of carotenoid-based plumage coloration is negatively affected by pigment access, general nutrition, and parasites. Thus, expression of carotenoid coloration encodes information about foraging success and health state. Experiments with a few species of passerine birds suggest that, in contrast to carotenoid coloration, melanin-based plumage coloration is less sensitive to the effects of nutrition and parasites during molt. Rather, melanin pigmentation seems to be shaped by social status. Thus, melanin pigmentation seems to be a signal of resource holding potential. These conclusions regarding the signal content of melanin and carotenoid feather coloration are based on experiments with a small number of songbird species and these ideas need to be confirmed in experiments with more species in different avian orders. Experimental evidence suggests that expression of melanin pigmentation functions in both mate choice and signaling social status, but that carotenoid coloration most commonly functions in mate choice. The evidence for females benefiting by choosing as mates males with the most elaborate carotenoid or melanin coloration is mixed. In several species of songbirds, males with more elaborate melanin or carotenoid coloration provide more food, but in other species there is no relationship or even a negative relationship between ornamentation and provisioning. Evidence that females gain genetic benefits by mating with males with elaborate carotenoid or melanin color displays is entirely indirect. The benefits to individuals of assessing plumage pigmentation in the context of intrasexual competition remain completely unstudied.

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Odors and Chemical Signaling

Julie C. Hagelin

3.1 INTRODUCTION

Ornithologists rarely consider the role of chemosensory information in avian reproduction. Yet, every bird that has been examined has a functional olfactory system (Bang and Wenzel 1985; Roper 1999). Like other vertebrates, birds detect and respond adaptively to odors in their environment while foraging (e.g. Nevitt *et al.* 1995, 2004; reviewed in Roper 1999), homing over long and short distances (e.g. Bonadonna and Bretagnolle 2002; Nevitt and Bonadonna 2005a,b; Wallraff 2004, 2005), and perhaps even avoiding predators (Fluck *et al.* 1996). There is also evidence that some avian species monitor the chemical environment of nests (Petit *et al.* 2002). However, compared to other organisms, information on the production or social use of self-produced odor compounds in birds has been largely neglected (Roper 1999).

The chemosensory abilities of birds stand as a promising means of understanding avian biology, because it challenges traditional views that birds respond to their world primarily through visual and auditory signals. Like other sensory systems, studies of the chemical senses are inherently interdisciplinary, as they involve responses at the molecular, physiological, developmental and behavioral levels. In particular, studies of avian-derived odors have the potential to fundamentally alter how we interpret social behavior. Social odors have been studied in other animals for decades, but, until recently, birds appeared to be the only vertebrate group that lacked them altogether (Wingfield *et al.* 1994). Thus, the chemical signals of birds represent an entirely new mode of avian communication that have the potential to reveal new and interesting aspects of behavioral ecology and sensory perception. They are akin to the startling discovery that some birds respond to ultraviolet plumage ornaments which humans cannot see (see Chapter 1).

This chapter has several goals. First, I examine the ways in which breeding birds adaptively employ odors derived from the environment, such as the use of odiferous plant materials in nests. The remainder of the chapter focuses in

detail on odors that birds produce themselves, as they relate to reproduction. I consider where avian-derived odors come from and how scent functions in social breeding contexts, with particular detail paid to two avian groups (petrels [Procellariidae] and auklets [Alcidae]) for which we presently have the most information. In view of recent developments, I highlight gaps in our basic understanding of avian odors and point out research areas that have proven quite productive in understanding the reproductive behavior of other animal systems, such as mammals. Finally, I propose a conceptual framework for future studies of avian chemical signals that addresses multiple levels of bird biology. To illustrate, I examine how olfactory anatomy can inform investigations that aim to understand how avian chemosignals function.

3.2 ODORS DERIVED FROM THE ENVIRONMENT

3.2.1 Plants

The nest site of breeding birds is an inherently dirty place, as it may contain ectoparasites, fungi, viruses and bacteria (e.g. Loye and Zuk 1991; Clayton and Moore 1997). Other organisms, such as invertebrates, regularly employ the chemical compounds of plants to protect themselves against harmful parasites, pathogens or predators (e.g. Rodriguez and Wrangham 1993; Berenbaum 1995), leading several authors to propose that the incorporation of certain types of herbaceous material into nests has an adaptive, or medicinal effect on avian residents. The “nest protection hypothesis” suggests that the volatile chemicals of plants produce a repellent or lethal effect on organisms harmful to birds (e.g. Wimberger 1984; Clark and Mason 1985; Clark 1991). Similarly, the “drug hypothesis” (Gwinner *et al.* 2000) suggests that, when inhaled or absorbed through the skin, plant compounds provide positive stimulation to the immune function of chicks, thereby reducing infection. Plant materials have been reported in the nests of several avian species, such as the House sparrow (*Passer domesticus*; Sengupta 1981), Wood stork (*Mycteria americana*; Rodgers *et al.* 1988), and Common buzzard (*Buteo buteo*; Roulin *et al.* 1997). However, I will focus on investigations of European starlings (*Sturnus vulgaris*) and the Corsican blue tit (*Cyanistes* (= *Parus*) *caeruleus ogliastreae*), as these are the most extensive, and provide both indirect and direct support for the two hypotheses listed above.

European starlings. *Sturnus vulgaris* and other passerines that reuse cavity nests for several seasons (and thus may suffer from higher parasite loads) are more likely to include green nesting material, compared to species that use a nest only once (Clark and Mason 1985). Despite an exceedingly small olfactory anatomy (see 3.7.1), *S. vulgaris* also responds (via cardiac conditioning) to the volatile compounds contained in the green plants that it prefers (Clark and Mason 1987a; Clark and Smeranski 1990). Herbaceous material also inhibited growth of bacteria and slowed the development of mites, a key

ectoparasite (Clark and Mason 1985, 1988). However, subsequent tests failed to measure the same effect on mites (e.g. Brouwer and Komdeur 2004; Gwinner and Berger 2005).

Interestingly, only male starlings add green plants to otherwise dry nest materials. The behavior primarily occurs during courtship and nest building, but discontinues after egg-laying (Pinxten and Eens 1990; Fauth *et al.* 1991; Gwinner 1997). Nests containing green materials are more likely to be chosen by females, indicating that the herbaceous components operate as sexually selected ornaments (Brouwer and Komdeur 2004; see also Soler *et al.* 1998). Although females respond to lower concentrations of some odor compounds than males (Clark and Mason 1987b), any olfactory cues involved in female choice (i.e. during nest building) are untested. Chemical assessment by the female of plant compounds contained in a male's decoration has been recently suggested in another avian species, however. Female Satin bower birds (*Ptilonorhynchus violaceus*) nibble at a mascerated plant-saliva mixture (called "paint") that males add to walls of their complex display arenas (Bravery *et al.* 2006).

For European starlings (*Sturnus vulgaris*), ornamental green plant material has a positive effect on reproduction. Gwinner and Berger (2005) provided direct evidence for the "nest protection hypothesis" from a five-year field manipulation in which experimental nests containing herbs produced heavier fledglings than those without, and late season nests with herbs exhibited reduced bacteria loads (Fig. 3.1; Wimberger 1984; Clark and Mason 1985; Clark 1991). The authors also observed that the mass and number of herbaceous plant species that males carried to nest sites changed over the course of two nesting events within a breeding season. Specifically, males brought more green material to their second (late-season) nest. Such a response is consistent with the enhanced infestation problems that second broods often face (Fig. 3.1B), and thus provides additional, indirect support for the "nest protection" hypothesis. More green nest material at second nests may also reflect greater effort on the part of the male to attract a second female (Gwinner and Berger 2005; Gwinner 1997). Though green plant material did not reduce numbers of mites at starling nests, it may interfere with blood sucking behavior (Gross 1975 as cited in Clark 1991), or stimulate certain aspects of a nestling's immune system (consistent with the "drug hypothesis;" Gwinner *et al.* 2000), which could be particularly advantageous during challenging environmental conditions (Gwinner *et al.* 2000, 2005).

Blue tits. Unlike *Sturnus vulgaris*, female blue tits (*Cyanistes* (= *Parus*) *caeruleus*), rather than males, frequently incorporate aromatic plant materials into the nest throughout egg laying and chick rearing (Lambrechts and Dos Santos 2000). On the island of Corsica, *P. c. ogliastreae* selects 6-10 aromatic herbs, including yarrow (*Achillea ligustica*), lavender (*Lavandula stoechas*) and mint (*Mentha suaveolus*), from more than 200 different plants identified on study plots (Petit *et al.* 2002). Furthermore, preferred herbs contained chemical

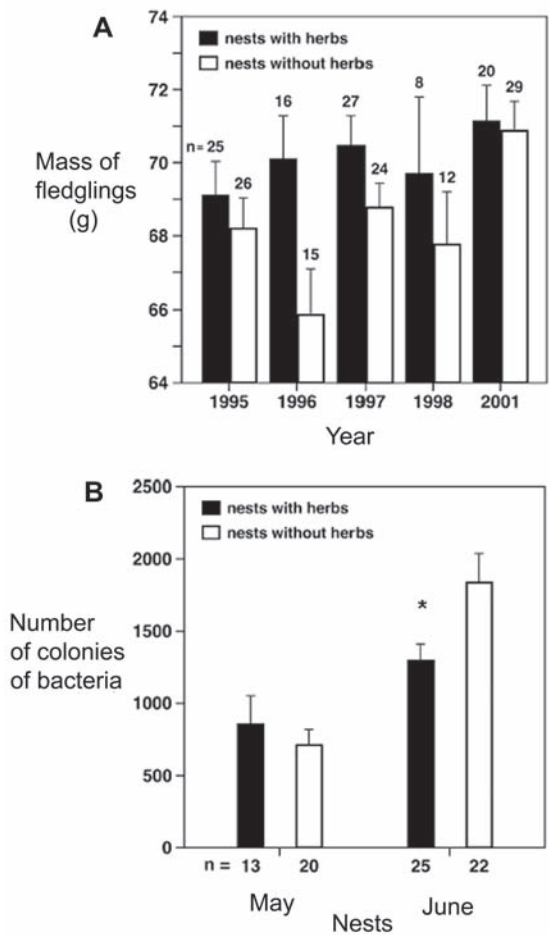


Fig. 3.1 **A.** Fledging mass of starling nestlings (*Sturnus vulgaris*) was greater in experimental nests containing herbs than those without. Specifically, mass was 2 g heavier in nests with herbs (General Linear Model: Nest type: $F_{1,120} = 12.0$ $P = 0.001$). **B.** Though infestation of bacteria increased between May and June nests (General Linear Model: Season: $F_{1,76} = 34.0$ $P = 0.0001$), the presence of herbs in experimental nests significantly reduced the bacteria load of June nests, as indicated (t-test: $t = -2.4$, $n = 45$, $*P = 0.02$). From Gwinner, H. and Berger S. 2005. *Journal für Ornithologie*. 146: 365-371, Figs. 6 and 4, respectively.

compounds known for repellent and antiseptic properties. The particular fresh herb fragments that females preferred also tended to lose their volatile compounds over a 48-hour period (Petit *et al.* 2002).

Petit *et al.* (2002) tested whether the odor of the nest environment stimulated females to replace fresh herb material. The investigators divided 64 nests (controlled for laying date, clutch size and chick age) into two equal treatments. In both treatments, the visual cues of herbs were removed from the

nests. However, aromatic cues were maintained in one set of nests by hiding fresh plant material (*A. linguistica* and *L. stoechas*) in a plastic cache attached to each breeding site. In the unscented treatment, nests lacked both herbs and odor, as the plastic caches were empty. Birds rapidly replaced herbs when scent was missing. However, where aromatic scent was maintained, birds only added herbs after 48 hours, consistent with natural odor depletion. Consequently, *Cyanistes caeruleus ogliastreae* monitored the scent of a nest in a manner consistent with maintaining a disinfected and/or ectoparasite-repellent environment (Petit *et al.* 2002). Like the behavior of *Sturnus vulgaris*, the results indirectly suggest that plant materials may function in “nest protection” (Wimberger 1984; Clark and Mason 1985; Clark 1991). Since the plants are highly aromatic to humans, the phenomenon has been specifically described for *C. c. ogliastreae* as the “potpourri hypothesis” (Lambrechts and Dos Santos 2000).

In contexts other than breeding, odor learning in adults of *Cyanistes caeruleus ogliastreae* has revealed some unexpected differences in response between the sexes (Mennerat *et al.* 2005). Namely, males, which do not build nests or help maintain an aromatic nest environment, were more attracted to feeder boxes emitting lavender odor than to odorless controls. Females, however, showed little difference in response to scented and unscented feeder boxes. The result was unexpected, as only females add scented materials to the nest (Petit *et al.* 2002). Nonetheless, there appear to be inherent sexual differences in behaviors related to odor learning when birds forage. Perhaps males are socially dominant to females at feeders, or maybe females are unable to associate odor with food rewards during the breeding season, while concurrently monitoring the scented environment of nests (Petit *et al.* 2002; Mennerat *et al.* 2005). Regardless, the interesting pattern is applicable to odor learning that occurs during the breeding season, and it is clearly worthy of future testing.

3.2.2 Heterospecific Animals

Common waxbills (*Estrilla estrilla*) of Africa add the odiferous products of other animals, namely carnivore scat, to their nests (Schuetz 2005). Similar to the Blue tit (*Cyanistes* (= *Parus*) *caeruleus*; see 3.2.1), *E. estrilla* adds scat throughout the nestling period, though it is unknown whether birds specifically monitor the aromatic environment at the nest. Scat reduces predation risk in both natural and experimentally manipulated nests, suggesting that it acts as an olfactory deterrent and/or chemical camouflage (Schuetz 2005). The incorporation of other kinds of heterospecific animal materials into nests, such as snake skin, has also been hypothesized as providing a similar benefit (Bolles 1890 as cited in Schuetz 2005). One might expect scat (or snake skin) to be a particularly potent deterrent when it is fresh, and volatile chemical components are most noticeable. However, it is currently unknown how or whether birds use odor cues to preferentially select certain types of nest items over others.

Heterospecific compounds are also employed in other ways, and may serve a hygienic function similar to that of plant materials in nests (see 3.2.1; reviewed in Dumbacher and Pruett-Jones 1996). For example, the poisonous *Pitohou* and *Ifrita kowaldi* of New Guinea have sour-scented feathers that contain neurotoxins, which are lethal to feather lice (Dumbacher *et al.* 1992; Dumbacher 1999; Dumbacher *et al.* 2000). Toxic compounds are likely derived from beetles in the diet (Dumbacher *et al.* 2004). Other avian species engage in “anting” or “defensive anointing,” the active daubing of chemicals from other organisms (i.e. ants) into plumage, which may also reduce parasites or pathogens (e.g. Ehrich *et al.* 1986; Moyer and Clayton 2003; Weldon 2004). However, unlike birds that use plant materials in nests, it is unclear whether this type of chemical warfare plays a heightened role during breeding or mate choice (for additional discussion see 3.4.5 and 3.5).

3.3 ODORS DERIVED FROM BIRDS

3.3.1 Odors, Chemical Signals and Pheromones

Aside from those naturally found in the environment, birds also produce a variety of odors themselves and, as we will see, some species are capable of recognizing and adaptively employing their scents. Throughout the text, I will refer broadly to the term “chemical signal” as any self-produced chemical compound or mixture that has a social or physiological effect on conspecifics (Johnston 2000). Investigators typically refer to conspecific odor as a chemical signal when intraspecific detection, recognition and/or transfer of information via odor stimuli has been demonstrated experimentally (Kavaliers *et al.* 2005).

The term “pheromone” is sometimes used interchangeably to describe any chemical signal (e.g. Wyatt 2003). However, its precise meaning has been the topic of some debate. Karlson and Luscher (1959) first defined a pheromone as a compound that, when present in minute quantities, is capable of eliciting an innate, stereotyped behavior, or other physiological or developmental process. Consequently, investigators often consider a pheromone to be a very specific kind of chemical signal, analogous to the ethological concept of a “sign stimulus” or “releasing stimulus” (Johnston 2000). Such a precise definition reduces ambiguity and lends itself to a specific set of testable predictions (e.g. Schaal *et al.* 2003). Since we are only just beginning to understand the role of odors and chemosignals in birds, it is, as yet, premature to claim that any avian odor signal functions as a pheromone (Hagelin *et al.* 2003).

3.3.2 Production of Avian Odors

Birds have a variety of glands (e.g. the preen or uropygial gland, anal gland, salt gland, as well as glands throughout the epidermis) that are capable of producing odors (Lucas and Stettenheim 1972; Jacob and Zisweiler 1982; reviewed in Waldvogel 1989). Avian scent also appears to be widespread. Odors that are readily detectable to humans occur throughout the class Aves

(19 orders, 80 genera; Weldon and Rappole 1997). A sub-sample of such groups is presented in Table 3.1. Likewise, odors derived from other avian sources, such as feces (Jones and Gentle 1985; Jones and Roper 1997), saliva (Bravery *et al.* 2006), stomach oils (Jouventin 1977; Wenzel 1985) and even conspecific blood (Jones and Black 1979) appear to be reasonable sources of chemical cues.

Table 3.1 Some avian orders considered very odorous by ornithologists. Data assembled from Weldon, P.J. and Rappole, J.H. 1997. *Journal of Chemical Ecology* 23: 2609-2632. Table 1.

Order	Common name	Number of species
Procellariiformes	Petrels, shearwaters, diving petrels	16
Ciconiiformes	Hérons, storks, New World vultures	12
Anseriformes	Ducks, geese, swans, screamers	49
Charadriiformes	Sandpipers, gulls, auks	23
Psittaciformes	Parrots	14
Cuculiformes	Cuckoos	16
Coraciiformes	Kingfishers, rollers, hoopoes, woodhoopoes	14
Piciformes	Woodpeckers, barbets, tucans	33
Passeriformes	Grackles, starlings, ravens, finches, honeycreepers	46

Human detection of avian scent clearly does not mean that an odor is important to a bird. However, early anatomical studies compared the uropygial gland, the primary source of secretions spread on plumage, to the scent glands of mammals and proposed that it produced odor signals (Pycraft 1910; Paris 1913 as cited in Jacob and Zisweiler 1982). Odiferous uropygial secretions of some seabirds, such as petrels and shearwaters (family Procellariidae), account for musky plumage scent, which readily rubs off onto other substrates (DeLeón *et al.* 2003; Bonadonna and Nevitt 2004). In other birds the gland size and the chemical components of uropygial secretions also vary by season (Kennedy 1971; Piersma *et al.* 1999; Reneerkens *et al.* 2002), sex (Jacob *et al.* 1979; Bhattacharyya and Chowdhury 1995), age class and diet (Sandilands *et al.* 2004a,b), suggesting that the chemical make-up and amount of secretions may differ depending on time of year or circumstance. Seasonal changes in odor have been quantified in one species (Table 3.2; Crested auklet [*Aethia cristatella*], Hagelin *et al.* 2003) and suggested in at least one other (Musk duck, *Biziura lobata*, Gamble 1966; see also 3.4.5).

Complex chemicals have been identified from the uropygial gland of numerous passerine and non-passerine species (Jacob and Zisweiler 1982; Reneerkens *et al.* 2002; Haribal *et al.* 2005) and are widely recognized as a means of chemical defense against feather parasites and pathogens (Jacob and Zisweiler 1982; Moyer *et al.* 2003; Shawkey *et al.* 2003). Long hydrocarbon chains of ester waxes are common, and substances appear to require frequent replenishment, as they degrade over time (Haribal *et al.* 2005). However, little

Table 3.2 Some volatile compounds of crested auklet (*Aethia cristatella*) plumage odor that vary in a seasonally significant manner. Data from Hagelin, J.C., Jones, I.L. and Rasmussen, L.E.L. 2003. Proceedings of the Royal Society. Series B: 270 1323-1329. Table 1.

Compound	Median concentration (µg/g feathers)	
	Breeding Season ¹	Winter
Octanal	2.98**	0.25
Z-4-Decenal	1.10**	ND
Hexanoic acid	0.84*	0.36
Octanoic acid	0.63*	0.15
Undecanal	0.35**	0.03
Z-2-Decenal	0.30**	ND
Tridecanal	0.30***	0.03
Octanol	0.18*	ND
Heptanal	0.15*	0.35

* P < 0.01, ** P < 0.005, ***P < 0.001

ND= not detectable in chemical analyses (< 0.0001 µg/g feathers)

¹Statistical significance is the result of a Wilcoxon two-sample test of scented feathers (breeding season) versus unscented (winter) feathers.

is known about the volatile compounds of uropygial secretions that make up avian-derived scent. In at least one species, the volatile fraction derived from uropygial secretions might repel predators. The cavity-roosting Green woodhoopoe (also known as the Red-billed woodhoopoe, *Phoeniculus purpureus*) turns away from a threat and produces a variety of foul-scented volatile compounds from its uropygial gland including several short-chain fatty acids, aldehydes, and dimethyl sulfide, which appear to act as a defensive secretion (Burger *et al.* 2004).

Aside from a direct connection between odor and uropygial secretions, it is important to note that some birds with striking feather scent actually produce uropygial secretions that are remarkably unscented. For example, Crested auklets (*Aethia cristatella*) emit a strong, citrusy plumage odor (Jones 1993), and a critically endangered parrot, the Kakapo of New Zealand (*Strigops habroptilus*), produces a distinctively sweet and musky odor (Hagelin 2004), but both birds produce uropygial secretions that are odorless to humans (personal observation). The volatile compounds that make-up the tangerine-like plumage odor of *A. cristatella* contain many simple hydrocarbons, including aldehydes and alcohols (Table 3.2). Though the odor source is unclear, the scent of *A. cristatella* is seasonal (Table 3.2), and does not differ strikingly between the sexes (Hagelin *et al.* 2003). Odor intensity, however, appears to vary between different captive populations (Douglas *et al.* 2001; Hagelin *et al.* 2003), suggesting that scent may be linked to diet or some other environmental factor.

Some avian scent appears to be derived from the chemical degradation of uropygial secretions. Namely, odor results from the breakdown of relatively complex and non-volatile compounds into strongly-scented acids and alcohols (Jacob and Zisweiler 1982: 306). Birds also host a diverse microbial community that may also play a role (Burt and Ichida 1999; Muza *et al.* 2000; Lucas and Heeb 2005). One Gram-positive, coccal bacterium, isolated from the uropygial gland of the green woodhoopoe, has been suggested to be involved in odor production (Laws-Brown 2001; Laws-Brown and Meyers 2003). It is also plausible that bacteria on plumage surfaces may be capable of producing odor (Hussain *et al.* 2005).

3.4 SOCIAL CONTEXTS OF AVIAN ODORS

3.4.1 Using Avian-derived Odors to Locate Home

Anyone who has visited a thriving colony of seabirds has undoubtedly noticed that the thousands of adults, young, and high concentrations of odiferous feces, all tightly packed into a small patch of breeding habitat, results in a potent olfactory experience. Procellariiform seabirds are well-known for their large olfactory bulbs relative to brain size (see 3.7.1; Bang and Cobb 1968; Bang 1971; Bang and Wenzel 1985), and for their response to food-related odors (Nevitt and Bonadonna 2005a,b; reviewed in Roper 1999). In particular, some birds, such as petrels and prions (Procellariidae), nest in areas with high densities of underground burrows and produce a musky plumage scent (Jacob and Zisweiler 1982; De León *et al.* 2003). Most return from sea after dark and several species appear to have poor night vision (Brooke 1989; Warham 1996), making their ability to locate the colony as well as their specific nest site rather remarkable (for discussion see Bonadonna *et al.* 2001; Bonadonna 2001). Some petrels even locate their burrow without the aid of song, as predation pressure at breeding sites can be intense (Warham 1996).

Pioneering studies by Grubb (1973, 1974, 1979) suggested that olfaction plays a role in the ability of Leach's storm-petrel (*Oceanodroma leucorhoa*) to correctly locate its burrow site in a colony of thousands. Grubb (1974) originally recognized that burrow odor may be involved when he discovered that birds consistently approached nest entrances from down wind. Bonadonna and Bretagnolle (2002) extended the work by manipulating the olfactory capacity of nine petrel species via two methods (plugging nostrils with putty, and injecting zinc-sulfate to temporarily destroy olfactory mucosa). The authors demonstrated that an intact sense of smell was especially important to successfully locating burrow sites in nocturnal species, but less so in diurnal species.

The environment in which petrels and other seabirds live can be visually featureless (open ocean) and inherently "noisy" when wind and waves obscure sight and sound. Consequently, avian-derived scent may not only function in locating a burrow, but perhaps also in navigation over longer

distances, such as returning to a colony, or locating large flocks of foraging conspecifics at dense patches of food. Both situations would appear to implicate homing to avian-derived scent in a manner similar to situations that involve prey-related odors (Nevitt and Bonadonna 2005b). On the foggy Bering Sea, for example, one can smell the citrusy scent of Crested auklets (*Aethia cristatella*) long before birds are visible (Sealy 2006; personal observation).

3.4.2 Discrimination of Own-Nest Odor

There is now ample evidence that several petrel species actively discriminate between the odor signatures of their own nest site relative to those of neighboring conspecifics (European storm-petrel, *Hydrobates pelagicus*; De León *et al.* 2003; Mínguez 1997; two prions, *Pachyptila* spp.; Bonadonna *et al.* 2003a,b; Blue petrels, *Halobaena caerulea*; Bonadonna *et al.* 2004; and two Diving petrels, *Pelacanoides* spp.; Bonadonna *et al.* 2003a). Even empty burrows are likely to emit the specific scent of inhabitants, as they contain feathers, feces (Bonadonna *et al.* 2003a,b) as well as body odor, which readily rubs off of a bird and onto other substrates (De León *et al.* 2003; Bonadonna and Nevitt 2004). Tests of burrow odor signatures have typically employed a T-maze apparatus, which can simultaneously examine, for example, whether birds distinguish between the scents of two different burrow sites (Fig. 3.2A). To prove that birds located their own nests by scent alone, investigators ruled out other, potentially confounding factors associated with burrow location by: (1) removing scented materials from burrows and placing them in an artificial setting (a metal box) attached to arms of the T-maze (Bonadonna *et al.* 2003a), (2) creating artificially displaced burrow entrances (Bonadonna *et al.* 2004), (3) positioning the arms of the maze into the original burrow entrances but blocking air (and thereby odor) movement (Bonadonna *et al.* 2003b, 2004), and (4) blocking a bird's own sense of smell (Mínguez 1997; Bonadonna *et al.* 2003b). In the first two cases, above, birds correctly located their own nest odor, but in the latter two they did not. It is important to note that the ability to recognize burrow scent extends to species with relatively unremarkable olfactory bulb sizes, such as diving petrels (Fig. 3.2B; Bonadonna *et al.* 2003a; see also 3.7.1), which also do not respond to food-related odors at sea (Lequette *et al.* 1989; Nevitt *et al.* 1995).

3.4.3 Discrimination of Self, Conspecific and Mate Odor

Burrows containing resident petrels have a noticeably strong scent, which is detectable to humans (Bonadonna and Bretagnolle 2002). Given a bird's ability to correctly locate its nest site using nest-odor cues alone, the next logical step was to test whether petrels distinguished between their own body odor, conspecific, or mate odor. Previous work suggested that Wedge-tailed shearwaters (*Puffinus pacificus*) experienced elevated heart rates when exposed to mate odor (Shallenberger 1975), although results were not particularly clear cut.

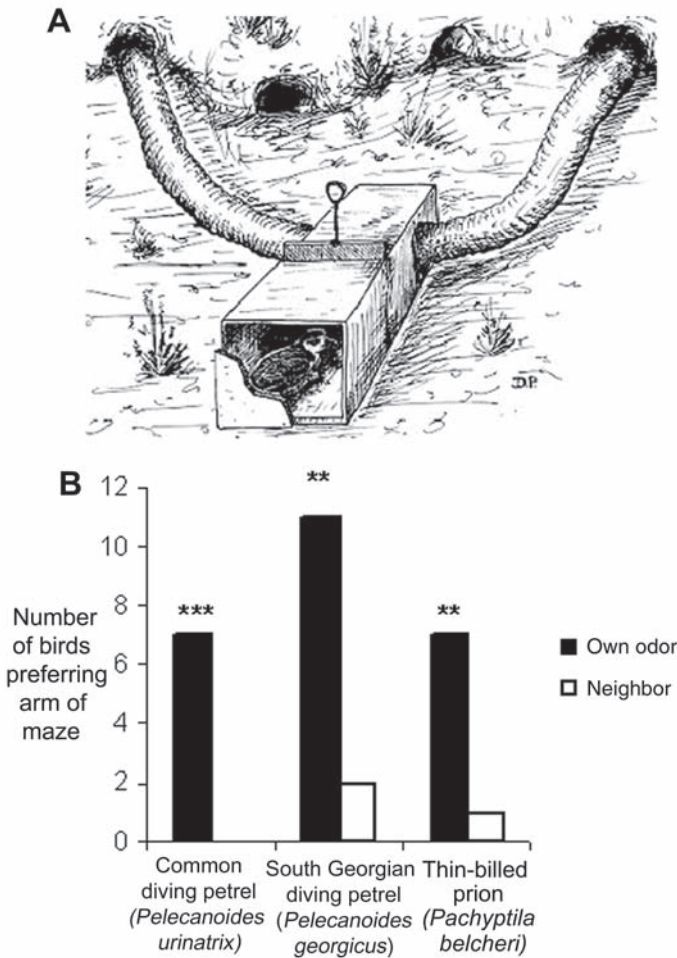


Fig. 3.2 Several species of petrels readily recognize the scent of their own burrow from that of a neighboring conspecific. **A.** Example of a T-maze test apparatus with arms that lead to two different burrows. Especially convincing results came from tests in which a maze was not connected to burrows, but contained nest materials only at the end of maze arms. **B.** Individual recognition of burrow odor has been demonstrated in diving petrels, which do not respond to food-related odors while foraging, as well as species that do, such as the thin billed prion. Significance indicates the preferences for home burrow odor in each species. *** $P = 0.008$, ** $P = 0.01$, * $P = 0.03$. From Bonadonna, F., Cunningham, G.B., Jouventin, P., Hesters, F. and Nevitt, G.A. 2003a. *Journal of Experimental Biology* 206: 3719-3722, Fig. 1; data from Table 1 were used to create 3.2B.

Using a Y-maze, Bonadonna and Nevitt (2004) discovered partner-specific odor recognition in Antarctic prions (*Pachyptila desolata*), a species that is philopatric to the same burrow and monogamous for life (Warham 1996). The

musky plumage odor used in the experiment was cleverly obtained by allowing scent to absorb into the cotton fabric bags in which birds were held. The results are striking (Fig. 3.3). Compared to the odor of a conspecific, resident birds were more attracted to the scent of mates, the odor of which is most likely to be in a burrow when a partner returns from sea (Fig. 3.3A; Bonadonna and Nevitt 2004). Birds also clearly recognized, and were attracted to, their own odor over a cloth bag control (Fig. 3.3B).

However, quite unexpectedly, and perhaps most importantly, Bonadonna and Nevitt (2004) discovered a pattern of scent recognition that is well-known in mammals. Namely, Antarctic prions *avoided* self-odor, when presented with the scent of a conspecific non-mate (Fig. 3.3C). The ability to recognize the scent of individuals, as well as distinguish self from non-self is a fundamental feature of behavioral organization (e.g. Thom and Hurst 2004; Tsutsui 2004). In particular, aversion to self-odor is a key component of complex social behaviors, such as inbreeding avoidance, and kin recognition which are well-known in mammals, particularly rodents (e.g. Mateo and Johnston 2000 but see Hare et al. 2003; Penn 2002; Kavaliers *et al.* 2005).

Inbreeding avoidance during mate choice may be especially important for species like *Pachyptila desolata*, which are philopatric and monogamous for life (see 3.5; Zelano and Edwards 2002, Bonadonna and Nevitt 2004). Self-referential phenotype matching (Mateo and Johnston 2000) would also appear to be a relevant mechanism for distinguishing kin from non-kin (Bonadonna and Nevitt 2004), as birds are long-lived and produce only one chick per season. Consequently, individuals may encounter potential mates later on in life that are unknown siblings (Mateo and Johnston 2000).

Further study is necessary to determine how body odor functions in breeding contexts and whether it is capable of providing other information, such as the sex of an individual (Bonadonna and Nevitt 2004). Behavioral data on individual or conspecific odor recognition in adults of other avian species are few, but worthy of future testing (see 3.5). Female domestic chickens, for example, appear to be unable to distinguish between familiar and unfamiliar conspecifics when visual cues are absent (Hauser and Huber-Eicher 2004).

3.4.4 Chicks, Parenting and Odor Learning

Similar to adult Antarctic prions (*Pachyptila desolata*), the chicks of European storm petrels (*Hydrobates pelagicus*) recognize their own body odor from that of a conspecific chick (De León *et al.* 2003). The ability to orient back to the nest is important to survival, as nests provide shelter and are the only location where chicks are fed. Evidence indicates that nest-specific odor cues assist chicks on their return (Mínguez 1997; De León *et al.* 2003). The general capacity of young birds to recognize a familiar body odor, however, does not appear to be restricted to petrels. For example, the behavior of juvenile geese exposed to parental scent versus control odors is indicative of an odor preference (Würdinger 1982). Domestic chicks (*Gallus domesticus*) also

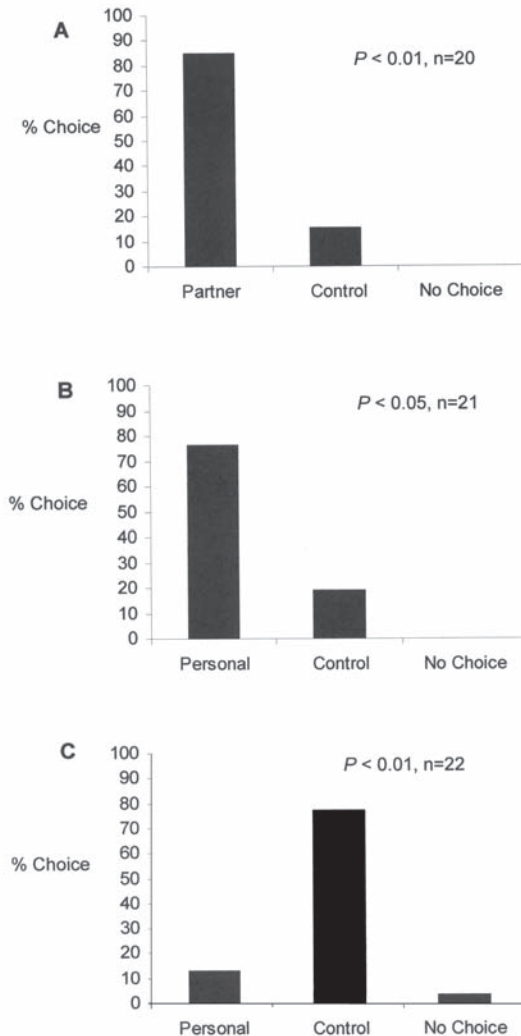


Fig. 3.3 Antarctic prions (*Pachyptila desolata*) show evidence of personal odor recognition and distinguish between odors of their mate (partner) and another conspecific. The figures above illustrate the results of three experiments. Each histogram indicates the proportion of birds that sought out a particular odor in Y-maze tests (or exhibited no choice). **A.** Birds preferred the scent of their partner over that of another conspecific. **B.** They also preferred their own personal scent over an unscented cloth bag control. **C.** Aversion to personal scent (and attraction to conspecific scent) is consistent with personal odor recognition and analogous to choice patterns of other vertebrates, such as mammals. From Bonadonna, F. and Nevitt, G.A. 2004. Science 306: 835-835. Data used in this figure came from Fig.1b-d.

preferentially orient toward the familiar scent of soiled bedding (Jones and Gentle 1985; Burne and Rogers 1995).

Studies of embryonic olfactory development in domestic chickens (e.g. Drapkin and Silverman 1999; Okano 1981), combined with tests involving artificial odor (e.g. Jones *et al.* 2002; Porter *et al.* 1999), are informative with regard to how chemical cues may function during development. For example, measurable differences in heart rate occur in embryos exposed to artificial odors (Tolhurst and Vince 1976). Furthermore, exposure to odors between embryonic day (ED) 15 through 20 (which includes the time period during which an embryo begins to breathe air), can result in post-hatching preferences for familiar scents (Sneddon *et al.* 1998; Porter and Picard 1998). Although it is currently unclear whether odor preferences can develop *in ovo* prior to ED 15, olfactory receptor neurons of chicks are functional at ED 13 (Lalloué *et al.* 2003).

The preference of domestic chicks (*Gallus domesticus*) for artificial odors that they experienced as embryos provides strong experimental support for odor learning. For example, after experiencing a novel scent (strawberry) in one of three ways (in the air, applied to the surface of the egg shell, or injected into the airspace of the egg), *G. domesticus* exhibited a greater affinity for (or weaker aversion to) wood shavings and water scented with strawberry, compared to control treatments (Sneddon *et al.* 1998). Chemosensory learning that occurs post-hatching can also enhance dispersal and readiness to feed, while reducing fear-related responses, indicating a calming or reassuring effect (Jones and Gentle 1985; Jones *et al.* 2002). In contrast, unfamiliar chemical cues can produce neophobic responses (Porter and Picard 1998; Burne and Rogers 1999; Jones *et al.* 2002; reviewed in Roper 1999). Both the embryos and newly-hatched chicks of *G. domesticus* are thus clearly capable of developing an odor familiarity or memory, which affects behavior later in life. Although the mechanistic details are presently unclear for birds, odor learning of embryos occurs in other animals (e.g. Semke *et al.* 1995), including humans (Schaal *et al.* 2000).

Combined, the data suggest that the ability of chicks to respond to, and possibly distinguish between, familiar nest or plumage odors occurs in at least two avian Orders. A preference for familiar odors may keep domestic chicks (*Gallus domesticus*) in close proximity to nests, or parents (Burne and Rogers 1995); a similar pattern is indicated above for petrel chicks (Mínguez 1997). The propensity for odor learning *in ovo* and post-hatching, combined with partner-specific odor recognition in adult prions (*Pachyptila desolata*; see 3.4.3), further suggests that birds may be capable of imprinting to odors associated with their natal site, as in some other vertebrates (e.g. Dittman *et al.* 1996; see also 3.7.3). Likewise, chicks may be capable of learning parental scent, or recognizing other siblings by scent in broods of multiple offspring (see 3.5.2; Zelano and Edwards 2002; Nakagawa and Waas 2004).

Conversely, the odors of chicks could also affect the responses of parents. Artificial odor added to offspring has been implicated in allocation of parental

care in the Rock dove (*Columba livia*; Cohen 1981). Though the role of bird-derived odors in chick rearing and chick development is not clearly understood, there is evidence for interspecific variation in response to food-related odors, which is both consistent with early odor learning in chicks, and the foraging responses of adults (Cunningham *et al.* 2003).

3.4.5 Odors Linked with Courtship or Other Displays

Balthazart and Schoffeniels (1979) reported the first evidence for the existence of an avian chemosignal during courtship, based on the differential responses of experimental and sham-operated male Mallards (*Anas platyrhynchos*). Experimental males had their olfactory nerves cut, rendering them unable to smell (anosmic). Anosmic males exhibited significant deficiencies in certain sexual and social behaviors relative to controls (Fig. 3.4). Furthermore, these males did not bathe or stand in water as frequently, which suggests that other, non-breeding behaviors may also be mediated by an intact sense of smell.

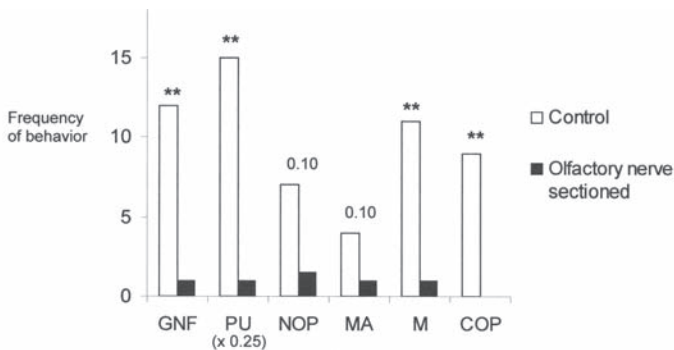


Fig. 3.4 Male mallard ducks (*Anas platyrhynchos*) exhibit responses consistent with olfactory detection of female chemosignals. Sexual displays of experimental males (olfactory nerve sectioned) were significantly inhibited compared to sham operated controls ($n=10$ of each). Data represent four hours of observation (16 sessions $\times$ 15min ea.) taken in January. Significance of Mann-Whitney U-tests for each display behavior is indicated (** $P < 0.01$, and $P = 0.10$). GNF: grasping neck feathers; PU: pumping toward female (difference in scale indicated); NOP: non-oriented pumping; MA: mounting attempt; M: mount; COP: copulation. Data adapted from Balthazart, J. and Schoffeniels, E. 1979. *Naturwissenschaften* 66: 55-56, Fig. 1.

The behavioral differences between anosmic and control males correlated with seasonal changes in the oil-gland chemistry of females, namely, the elevation of diester waxes (Jacob *et al.* 1979, Bohnet *et al.* 1991). The results therefore suggest that male mallards detect important chemosignals in the scent of the opposite sex. Despite intriguing evidence, the process of odor transmission during mallard courtship (or that of other species) is generally unclear, making changes in a male's behavioral repertoire somewhat difficult to interpret.

Displays of crested auklets. The Crested auklet (*Aethia cristatella*), a highly social, planktivorous seabird of the western arctic, produces an unusual, tangerine-like or citrusy plumage odor during the breeding season that is associated with a striking, seasonal behavior. Individuals engage in a frequently repeated “ruffsniff” display, in which birds place their bills within the nape feathers of a display partner, a region that appears to be strongly scented (Fig. 3.5; Jones 1993; Jones and Hunter 1993; Hagelin *et al.* 2003). The ruffsniff suggests a behavioral means of acquiring chemosensory information via odor assessment and/or scent marking others (Hagelin *et al.* 2003). During the breeding season *A. cristatella* display on rocks and nest in crevices of talus slopes; adults rear a single, semiprecocial chick that is provisioned by both parents (Jones 1993).

Though no striking chemical differences exist between males and females (Hagelin *et al.* 2003), the odor of *Aethia cristatella* exhibits several features consistent with a social chemosignal. First, scent is produced seasonally by both sexes (Table 3.2). Second, scent is associated with the striking ruffsniff display behavior (described above) that appears to be a self-evident means of odor assessment. Third, experimental manipulation of odors in T-maze experiments and on realistic taxidermy models revealed that individuals distinguish between, and respond preferentially to, the odor of natural plumage, and a synthetic mixture of key, seasonally-elevated odor compounds (Figs. 3.6-3.7; Hagelin *et al.* 2003; Jones *et al.* 2004).

Though Hagelin *et al.* (2003) reported a difference in scent between summer and winter birds (Table 3.2), more recent observations indicate that odor varies within the summer breeding season. Weeks before arriving at a colony, birds are noticeably unscented (Sealy 2006). In both wild and captive populations, concentrations of key odor compounds (octanal, Z-4-decenal) were greatest early in the season (June), but dropped two to six fold by the end of the season (August; unpublished data). Odor loss coincided with the loss of secondary sexual ornaments (crests, orange beak plates; personal observation), suggesting that seasonal variation in odor production is related to hormonal changes. Within-season odor loss, combined with the proclivity for *Aethia cristatella* to engage in mutual sexual selection for other plumage traits (i.e. crests; Jones and Hunter 1993, 1999), indicates that scent may function as an olfactory ornament (Jones 1993; Hagelin *et al.* 2003; Douglas *et al.* 2005a).

Social function of crested auklet odor. Field tests of a synthetic odor mixture (cis-4-decenal and octanal) added to the plumage surfaces of realistic taxidermy models revealed insight into the social function of *Aethia cristatella* odor (Jones *et al.* 2004). Scent had the greatest social effect in the context of the male sex. Both male and females approached scented male models more closely than controls; no such pattern was evident for scented female models (Fig. 3.7; Jones *et al.* 2004). Furthermore, synthetic scent applied to male models evoked enhanced interest from approaching males only. Males more frequently stayed



Fig. 3.5 During the “ruffsniif” display of Crested auklets (*Aethia cristatella*), individuals place their bills within a display partner’s nape feathers, a region of the body that is strongly scented. Displays can be intersexual or intrasexual, involving two birds (A), or more (B). Photographs: I.L. Jones and J.C. Hagelin. Fig. 3.5A from Hagelin, J. C., Jones, I. L. and Rasmussen, L. E. L. 2003. Proceedings of the Royal Society Series B 270: 1323-1329, Fig. 1.

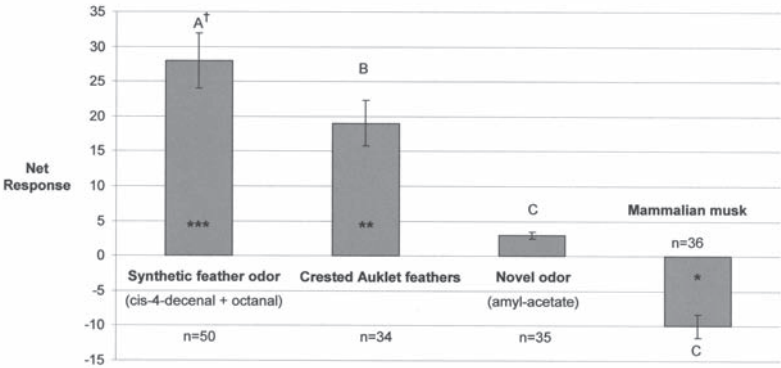


Fig. 3.6 In T-maze experiments, crested auklets (*Aethia cristatella*) were attracted to synthetic plumage odor and to natural plumage scent, but were repelled by mammal musk. Net response indicates the percent time a bird spent in the odored arm of the T-maze minus the control arm. Data represent means $\pm$ standard error. Asterisks within each bar indicate the results of a paired t-test that examined whether the net response (odor minus control) was significantly different from zero. There was no significant response to a novel odor (amyl-acetate [banana scent]). * P (two-tailed) = 0.02, ** P = 0.006, *** P = 0.0004. Different letters above bars indicate significant differences in net response between odor treatments: $0.006 < P$ (two-tailed) < 0.02 . Data adapted from Hagelin, J.C., Jones, I.L. and Rasmussen, L.E.L. 2003. Proceedings of the Royal Society Series B 270: 1323-1329, Fig. 2. †Net response to synthetic feather odor (a more concentrated scent than plumage odor) was greater than the net response to natural plumage odor P (one-tailed)= 0.042. A one-tailed test was used, as the authors made the directional prediction that birds would be more attracted to stronger auklet scent.

for durations greater than 10 seconds in front of scented male models than unscented controls, but females did not (Jones *et al.* 2004).

Intrasexual aggression between males is emphasized in *Aethia cristatella*, as males jockey for position at prime display locations (Jones 1993; Gaston and Jones 1998; Jones and Hunter 1998). Though both sexes engage in territorial disputes (Jones *et al.* 2004), males usually retain the nest site from year to year (e.g. Zubakin and Zubakina 1994) and actively defend it during laying (personal observation). In *A. cristatella*'s dark, underground nesting environment, odor could therefore serve as a reliable cue of an approaching aggressor, as males can displace residents from crevices (personal observation). The chemical concentration of at least one odor compound correlated positively with the social status of captive males, further indicating a link between odor and male behavior (unpublished data). At present, the data suggest that odor serves at least a general social function in *Aethia cristatella* (Jones *et al.* 2004). Further tests are required to clarify the role of odor in the context of male-male competition.

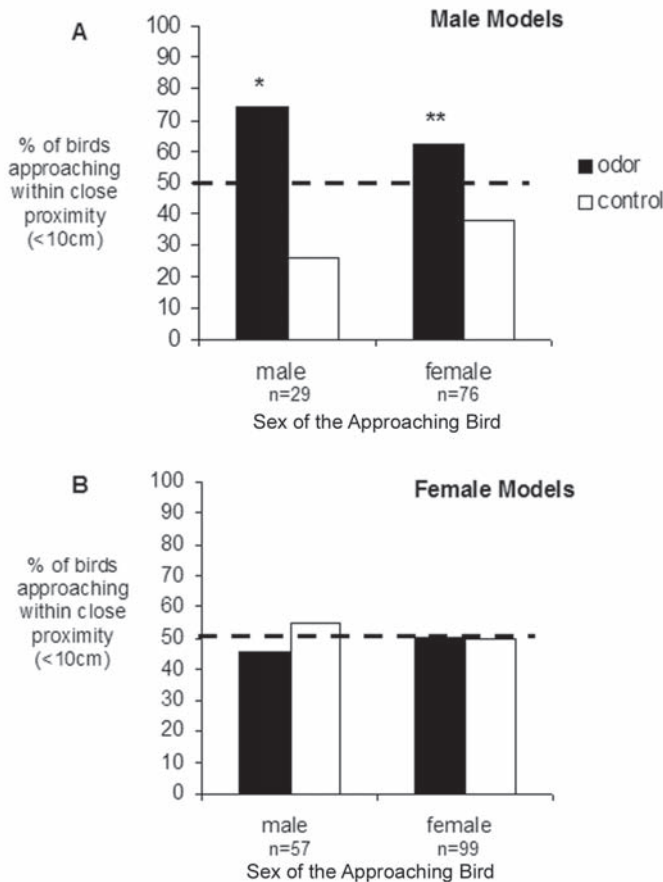


Fig. 3.7 **A.** Male models treated with synthetic citrus odor were approached significantly more often than unscented models by both male and female crested auklets (*Aethia cristatella*). **B.** No differences were detected for birds approaching scented female models. Dashed line indicates the null expectation of equal approach frequency. ** $P = 0.02$, * $P = 0.04$. Figure created from data in Jones, I.L., Hagelin, J.C., Major, H.L. and Rasmussen, L.E.L. 2004. Condor 106: 71-78, Table 1.

Synthetic odor does not elicit ruffsniiff displays on approach. Interestingly, field tests of synthetic scent applied to *Aethia cristatella* models failed to increase the frequency of ruffsniiff displays (or any other sexual behavior) of approaching birds (Jones *et al.* 2004). Such results indicate that odor may be employed in a more complex, or multi-modal fashion, in which a combination of olfactory, visual and/or auditory cues evokes a response, or, perhaps, odor is not involved in displays. Unlike synthetic odor, experimental manipulation of crest size on models increased the rates of sexual display behavior of wild birds by two to fourfold (Jones and Hunter 1993; Jones and Hunter 1998).

Combined, the data suggest that approaching birds respond more readily to visual than to odor cues (Jones *et al.* 2004).

As one bird approaches another, the crest, rather than odor, would appear to be a more reliable signal, given that both wind speed and direction on top of display rocks are quite variable, and could thereby reduce detection of an olfactory signal. Instead, scent may be assessed at much closer range (i.e. on contact), when birds engage in ruffsniff and neck-twist displays (Jones *et al.* 2004). Future tests of captive birds that use more complex odor mixtures and examine interactions between visual and odor cues (e.g. Osterbauer *et al.* 2005), may prove more successful than inanimate models treated with only two synthetic odor compounds (Jones *et al.* 2004).

Repellent properties of crested auklet odor. Douglas *et al.* (2001) proposed that crested auklet odor may serve as an honest indicator trait during sexual displays (see Chapters 2, 4 and 5), because the odor contains aldehydes that are chemically similar to some invertebrate repellents. Thus, a more strongly scented individual may be advertising its ability to combat parasites or possibly pathogens on itself or perhaps the chicks it broods. This idea is analogous to the hygienic properties of plants or other heterospecific toxins (see 3.2.1 and 3.2.2).

Ectoparasites on feathers and skin do not appear to be problematic to most adult *Aethia cristatella* (Douglas *et al.* 2004). However, young birds, which are noticeably unscented (Sealy 2006), are occasionally infested with lice and ticks (Douglas *et al.* 2005a; personal observation). Experimental tests examining the defensive properties of plumage odor on ectoparasites have produced mixed results. Volatiles from freshly plucked feathers failed to reduce the survivorship of feather lice (Douglas *et al.* 2005a). Ticks, collected at an auklet breeding colony (*Ixodes uriae*) and subjected to 24 hour dyadic choice test in petri dishes, were also just as likely to prefer scented as unscented feathers (Fig. 3.8). Auklet odor is highly volatile (Douglas *et al.* 2004), and fresh plumage can lose its potency in a matter of days (Hagelin *et al.* 2003), which might explain the lack of repellency for tests involving natural feathers. Although the source of odor is unclear, live birds presumably re-apply scent through frequent preening.

Unlike tests of natural feather odor, those involving synthetic odor compounds (e.g. octanal, Z-4-decenal) have repelled two species of ticks (including *Ixodes uriae*; Fig. 3.9; Douglas *et al.* 2004), mosquitoes (Douglas *et al.* 2005b), and greatly increased mortality in two genera of auklet feather lice (*Quadriceps*, *Austromenopon*; Douglas *et al.* 2004). Though the results are consistent with scent acting as an honest indicator trait with regard to chemical defense, some chemical treatments exceeded the natural odor concentration of fresh plumage. For example, Douglas *et al.* (2004) placed 1 μ l (or 850 μ g) of Z-4-decenal on a single auklet feather, which caused feather lice to become moribund within seconds. This amount of odor is approximately 68,000-960,000 times that of natural plumage. The calculation is based on two pieces of information: (1) A single nape feather weighs approximately 0.0008 g (n=10),

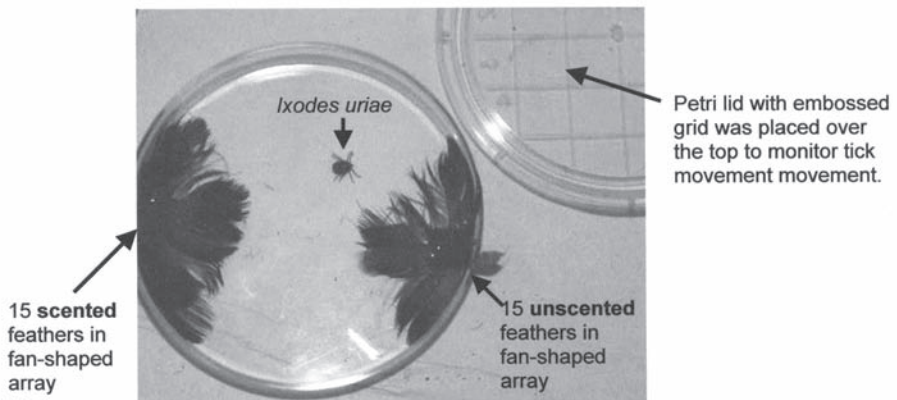


Fig. 3.8 Ticks (*Ixodes uriae*) collected at a crested auklet colony (*Aethia cristatella*) were placed in the center of a petri dish and given a 24 hour “choice” to climb into fresh, scented feathers of (*A. cristatella*) or unscented feathers (of parakeet auklets [*A. psittacula*; $n = 45$ trials] or least auklets [*A. pusilla*; $n = 45$ trials]). Plumage odor did not appear to act as a repellent, as 49 ticks chose scented feathers, and 41 chose unscented feathers ($\chi^2 = 0.71$, $df = 1$, $P = 0.40$). Plumage from each unscented species lacked chemical compounds found in *A. cristatella* odor (*A. psittacula*, Hagelin *et al.* 2003; *A. pusilla*, unpublished data).

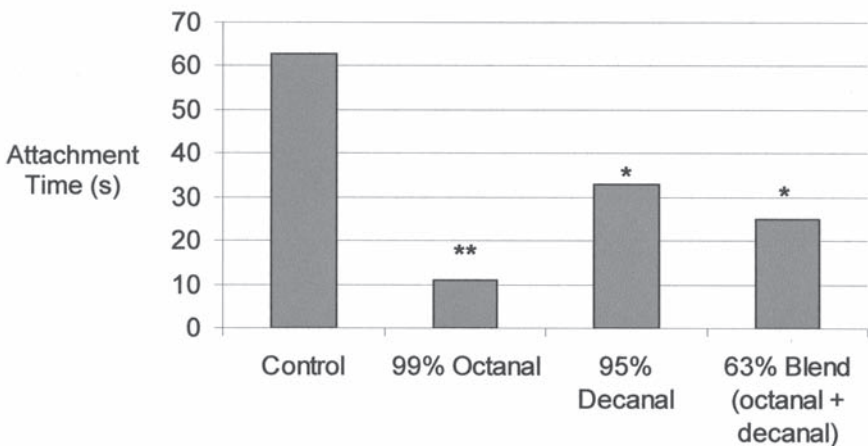


Fig. 3.9 Ticks (*Ixodes uriae*) that parasitize crested auklets (*Aethia cristatella*) were repelled more readily from a paper substrate treated with synthetic odor than an ethanol control. Mean attachment time is given for four treatments, each of which tested 30 ticks in a moving object bioassay (Dautel *et al.* 1999). Significant differences between each treatment and the control are indicated. Odor treatments consisted of synthetic compounds dissolved in ethanol. Adapted from Douglas III, H.D. Co, J.E., Jones, T.H. and Conner, W.E. 2004. *Journal of Chemical Ecology* 30 (10): 1921-1935. Fig. 5. * $P < 0.05$ ** $P < 0.01$.

and (2) The median concentration of Z-4-decenal in the nape region has been estimated between 1.1 μg (Table 3.2; Hagelin *et al.* 2003) and 15.5 μg (unpublished data) per gram of feather weight.

A somewhat more compelling argument can be made for the repellent effect of synthetic odor on ticks. Douglas *et al.* (2004) used a moving object bioassay (Dautel *et al.* 1999) to assess the attachment time of ticks to a filter paper treated with synthetic compounds and odor blends. The authors reported a pattern consistent with dose-dependent repellency, namely, reduced attachment times with increasing odor concentration. The concentrated odor treatments (e.g. 99% octanal; Fig. 3.9), applied to a relatively small surface area of paper (7.6 cm x 3.2 cm), in some cases hourly, appear to have been equivalent in concentration to 5 to 14 adults. My calculations are based on: (1) the concentration of natural plumage odor (2.98 μg octanal/g of feathers; Table 3.2; Hagelin *et al.* 2003), (2) the density of octanal (0.843 g/ml), (3) the volume of the solution tested (0.008-0.025 ml/cm² of filter paper; Douglas *et al.* 2004), and (4) the average dry weight of adult plumage (11.93 g; n=5 adult *Aethia cristatella*, unpublished data).

However, it is equally important to note, that the median concentration of octanal in nape feathers appears to be rather variable (53 μg /g of feathers in another population; unpublished data). Thus, the concentrated treatments of Douglas *et al.* (2004) may have mimicked odor intensities that were ecologically relevant. Furthermore, less-concentrated treatments, such as a 63% synthetic blend (Fig. 3.9) and a 1% dilution (see Douglas *et al.* 2004) also repelled ticks successfully, lending additional experimental support for certain odor compounds acting as a chemical defense.

If the odor of *Aethia cristatella* functions as a chemical defense, either as an honest indicator trait in adults and/or a means of protecting unscented chicks, it does not have an immediate, lethal impact on parasites like the toxins of *Pitohou* feathers (Dumbacher 1999). Rather, natural concentrations of odor appear to have repellent or sublethal effects. It is unknown, however, how the scent of *A. cristatella* may interfere with or impair the physiology of ectoparasites (Douglas *et al.* 2005a). Preliminary tests indicate that some synthetic compounds of *A. cristatella* odor inhibit the growth of bacteria (such as *Salmonella*; unpublished data), consistent with other avian secretions (Shawkey *et al.* 2003).

Other species and observations. The role of scent during courtship or territorial displays had been suggested, but untested, in other birds, such as the Musk duck (*Biziura lobata*) of Australia, in which adult males produce a musky scent during the breeding season only (Gamble 1966). Likewise, Bulwer's petrel (*Bulweria bulwerii*) emits an unusual odor during pre-laying that could act as a mating signal (Thibault and Holyoak 1978). Snow petrels (*Pagodroma nivea*) also regurgitate odiferous stomach oils at nest entrances during territorial disputes (Jouventin 1977). Many birds regularly engage in social behaviors, such as mutual preening, which potentially exposes them to odors of mates or other conspecifics (Roper 1999). Greater shearwaters

(*Puffinus gravis*), in particular, nibble at the uropygial gland during allopreening (Hagen 1952 as cited in Roper 1999).

Careful observations of the olfactory system of European starlings (*Sturnus vulgaris*) indicated an elevated sensitivity to odors during the breeding season (Clark and Smeranski 1990), which also correlated with changes in beak color (Clark and Mason 1987b). Thus, chemical cues may be especially important during breeding months and appear to reflect changes in sex hormones. Such a pattern is consistent with the seasonality of scent and display behaviors in crested auklets (*Aethia cristatella*; see **Displays of Crested Auklets**), Mallards (*Anas platyrhynchos*; Balthazart and Schoffeniels 1979; Jacob *et al.* 1979, Bohnet *et al.* 1991), and the chemical changes in odor and glandular secretions of other species (see 3.3.2).

3.5 IMPLICATIONS OF AVIAN ODOR AS A SIGNAL

The links between genes, odor, and complex social behavior are well-documented in animals, especially in rodents (reviewed in Penn and Potts 1998; Beauchamp and Yamazaki 2003; Hurst and Benyon 2004; Kavaliers *et al.* 2005; Ziegler *et al.* 2005). For example, volatile chemosignals mediated by alleles of the major histocompatibility complex (*Mhc*) play a key role in sexual and social behaviors of mammals and fish (Reuch *et al.* 2001; Penn 2002; Aeschlimann *et al.* 2003; Beauchamp and Yamazaki 2003; Kavaliers *et al.* 2005), but have been largely overlooked in birds (Zelano and Edwards 2002). Odors mediated by *Mhc* can be pathogen-driven, and thus indicative of infection, or they may relate to non-pathogenic mechanisms, such as selection for inbreeding avoidance (reviewed in Zelano and Edwards 2002). Such signals are applicable to both “good genes” models of sexual selection (see Chapter 6) and those that emphasize genetic compatibility (Mays and Hill 2004; Neff and Pitcher 2005). However, any odor cues that may drive such behaviors in birds are unknown.

3.5.1 A General Role for Honest Odor Signals in Birds?

Just as rodents use odor to detect parasitized or infected conspecifics, assess age, sex, social status or kinship, avian scent (or other chemical secretions) may also act as an “honest indicator” trait (reviewed in Andersson 1994; Penn and Potts 1998, 1999; Penn 2002; Beauchamp and Yamazaki 2003; Zala *et al.* 2004; Kavaliers 2005). Consequently, bird-derived odor could form the basis of secondary sexual traits (Hagelin *et al.* 2003), similar to the way in which bright plumage, complex song, or ornamental green nesting material correlates with reduced pathogens, parasites, or enhanced offspring survival (e.g. Zuk 1993; Gwinner and Berger 2005; Spencer *et al.* 2005; see 3.2.1, 3.2.3 and Chapters 5 and 6 for additional discussion). Furthermore, links between visual stimuli (colors) and scent perception (e.g. Cooper *et al.* 1994; Osterbauer *et al.* 2005) have interesting implications for complex or multimodal signals involving avian odor, as birds show a heavy reliance on visual cues. With

regard to patterns of odor and choice, one might expect positive or negative responses, depending on circumstance.

Positive relationships between odor and choice. Compounds used as chemical defenses in some birds appear to be derived from the diet (Dumbacher *et al.* 2004; see also 3.2.2), similar to visually-mediated plumage ornaments like carotenoid pigments (Hill 2002; and Chapter 2). The magnitude of direct or indirect benefits associated with such compounds may therefore correlate positively with odor concentration. This would be especially true if odorous compounds have antiseptic or anti-parasitic properties, as suggested for some toxic species in the genus *Pitohoui* (Dumbacher 1999) as well as the citrusy scent of crested auklets (*Aethia cristatella*; Douglas *et al.* 2001, 2005a,b; Hagelin *et al.* 2003). Feather lipid concentration may act as an honest signal, as it is related to age in domestic chickens (*Gallus domesticus*); age and bird growth are also related to the development of the uropygial gland, which provides secretions that birds spread over feather surfaces (see 3.3.2; Sandilands *et al.* 2004a,b).

Negative relationships between odor and choice. Aversive odors in birds have been linked to the scent of blood and feces (Jones and Gentle 1985; Jones and Roper 1997; Jones *et al.* 2005). In rodents, however, chemical aversion can be pathogen driven, as odors correlate with parasitized individuals, or they can be indicative of genetic incompatibility (reviewed in Penn and Potts 1998, 1999; Penn 2002; Beauchamp and Yamazaki 2003; Kavaliers *et al.* 2005).

One of several general functions attributed to non-volatile secretions of the avian uropygial or preen gland is an ability to combat bacteria (or other ectoparasites, such as lice) and to keep feathers clean (Jacob and Zisweiler 1982; Shawkey *et al.* 2003; Haribal *et al.* 2005). Clean and well-preened feathers clearly look different than dirty feathers. However, evidence from domestic chickens (*Gallus domesticus*) also suggests that odor cues may be involved. For example, birds responded differentially to feathers that contain oils from the uropygial gland (McKeegan and Savory 2001). Furthermore, feather lipid concentrations were greatly affected by the presence or absence of a dustbathing substrate (Sandilands *et al.* 2004b), suggesting that compounds spread onto feathers may also correlate reliably with hygiene.

The production of avian odor has been hypothesized to result from the breakdown of non-volatile preening compounds (Jacob and Zisweiler 1982), either via natural degradation or in combination with ectosymbionts, such as bacteria or feather lice (Haribal *et al.* 2005). Hence, low-levels of plumage scent (or the lack of a particular compound that is associated with pathogenic infection), may reflect the ability of a bird to successfully clean its feathers via frequently re-application of non-volatile secretions. Reduced feather scent could be particularly adaptive for a breeder that must remain chemically “inconspicuous” in the face of mammalian predation (Reneerkens *et al.* 2002). An aversion to certain odors, such as the scent of self in Antarctic prions (*Pachyptila desolata*), also has implications for studies of genetic compatibility (see 3.4.3, 3.5.2; Bonadonna and Nevitt 2004).

The potential for hypothesis testing of avian odors, as they relate to honest signaling, pathogens, sex, status, age and/or genetic compatibility is rather extraordinary. Future studies will require an understanding of: (1) odor-mediated choice as it relates to parasites, infection and genetic compatibility, (2) conspecific variation in odor signatures relative to sex, age and social status, (3) the ecology of plumage ectosymbionts and their role, if any, in odor production, and (4) a detailed chemical understanding of volatile and non-volatile compounds in avian odor that may result from the diet, natural chemical degradation and/or the glandular secretions themselves.

3.5.2 Prospects for Odors Related to Kin Selection and Mating System

Kin selection. Aside from pathogen-mediated scent, the odor of rodents has profound ties to kin recognition. For example, *Mhc*-mediated odor profiles of mice can influence mate choice (via disassortative mating and inbreeding avoidance), individual recognition, nesting patterns, and selective block of pregnancy (reviewed in Penn 2002; Beauchamp and Yamazaki 2003; Ziegler *et al.* 2005). The interesting discovery that adults and chicks of some petrels species distinguish between odors of self and other conspecifics (see 3.4.3, 3.4.4), paves the way for more in-depth studies (Bonadonna and Nevitt 2004; Nevitt and Bonadonna 2005a). Given the marked odor of some species that are well-known for cooperative breeding, such as the green woodhoopoe (*Phoeniculus purpureus*; du Plessis 1992; Ligon and Ligon 1978; Burger *et al.* 2004), the prospects of odor affecting the social interactions between kin would also appear fruitful.

Mating system. Zelano and Edwards (2002) suggested a number of mating situations in which *Mhc*-mediated responses of birds are likely to occur. Such environments appear to be generally good places to search for avian-derived odor signals, given the links between odor and mate choice in other vertebrate groups (see 3.5). The authors highlighted long-lived species, such as seabirds and raptors, which may be subject to inbreeding or exhibit lifetime monogamy. Both characteristics have enhanced consequences for mate choice based on good genes and/or genetic compatibility. Evidence for discrimination between the plumage odor of self, mate and other conspecifics has already been discovered in one avian species (see 3.4.3; Bonadonna and Nevitt 2004).

Likewise, lek mating is expected to be linked to females that focus on the indirect (genetic) benefits of males that typically provide no parental care. One notable lek breeder with seasonally elevated scent in males only is the musk duck (*Biziura lobata*; Gamble 1966; McCracken *et al.* 2000; Guay and Mulder 2005). Another species, the critically endangered kakapo of New Zealand (*Strigops habroptilus*) might also employ odors in its unusual lekking system (see 3.5.3; Eason *et al.* 2006). Odor function in any lek breeding system, however, is unstudied.

Finally, Zelano and Edwards (2002) suggested that *Mhc*-mediated responses are applicable to situations in which birds may choose from many

prospective mates or engage in extra-pair fertilizations. Genetic patterns attributable to *Mhc* have been implicated in avian sexual selection and reproductive behavior (e.g. von Schantz *et al.* 1996; Freeman-Gallant *et al.* 2003). Though the role, if any, of odor is unknown, some data suggest that females may select extra pair mates in a manner consistent with inbreeding avoidance and selection for genetically dissimilar mates (e.g. Richardson *et al.* 2005; Tarvin *et al.* 2005, but see Smith *et al.* 2005). More studies are necessary to examine whether avian scent correlates with extra pair mate choice and exhibits odor-mechanisms similar to those of mammals.

3.5.3 Applied Problems and Species Recovery

Bird responses to odors have already provided useful information applicable to situations involving animal welfare and captive breeding, such as the poultry industry (reviewed in Jones and Roper 1997, Jones T. A. *et al.* 2005). For example, exposure to concentrated ammonia from feces, can reduce egg laying capacity and growth rates of domestic chickens (*Gallus domesticus*; Reese *et al.* 1980; Hester 2005; Jones E. K. M. *et al.* 2005). Familiar odorants, however, can reassure or attract birds (see 3.4.4; Burne and Rogers 1995; Jones *et al.* 2002). One extreme example involving an aberrant attraction to plumage, chronic feather pecking, has been linked to uropygial secretions on feather surfaces (McKeegan and Savory 2001). Avian scent is also related to reproductive contexts, such as courtship and nesting (see 3.4, 3.5.2; Hagelin *et al.* 2003; Bonadonna and Nevitt; 2004). Consequently, it may be feasible to apply our knowledge to species recovery, particularly in management situations that aim to increase the breeding success of captive or endangered populations.

Avian-derived odors or unusual chemical substances have been implicated in at least two critically endangered species: (1) the Kakapo, a parrot endemic to New Zealand (*Strigops habroptilus*; Hagelin 2004) and (2) the Toki, or Japanese crested ibis (*Nipponia nippon*; Wingfield *et al.* 2000). *S. habroptilus* is nocturnal, solitary and unusually scented; plumage odor is detectable (to humans) from a distance of 6 m (Hagelin 2004). Birds also have a large olfactory anatomy, respond to olfactory cues while foraging (Hagelin 2004). Furthermore, *S. habroptilus* exhibits an unusual lek breeding system (Merton *et al.* 1984), in which odor could provide a means for *Mhc*-mediated mate choice (see 3.5.2; Zelano and Edwards 2002; Eason *et al.* 2006). If birds detect feather scent, the data suggest they may be capable of employing it to sense and/or assess conspecifics in their vicinity. Scent would appear to be particularly applicable to facilitating the successful management of infrequent breeding events, which occur every two to seven years (Hagelin 2004; Eason *et al.* 2006).

The Toki (*Nipponia nippon*) secretes a tar-like substance from a discrete patch of skin in the neck and throat region. The substance is actively spread on the head, neck and torso, resulting in specialized nuptial plumage (Wingfield *et al.* 2000). Such ornamentation probably provides visual as well as chemical information to prospective mates or competitors (J. Wingfield, personal communication). The tar-like secretion is only found in adults, and

successful breeding is related to hormone levels (Wingfield *et al.* 2000). Hormone therapy applied to failed breeders, which could facilitate gonadal development, egg-laying, and presumably the acquisition of nuptial plumage, has been suggested as a means of promoting reproduction in this species (Wingfield *et al.* 2000).

3.6 CALL FOR A MULTIDISCIPLINARY APPROACH

Despite a number of interesting studies and intriguing prospects, biologists currently lack a basic framework for studies of avian chemosignals. The problem exists, because we know relatively little about the context(s) in which odors are actually used in birds, the structures and mechanisms of the anatomy that perceives odors, and the details of odor chemistry. Studies that integrate multiple disciplines have proven extremely useful in other vertebrate groups (e.g. Sorenson 1996), because the chemosensory signaling process involves an interrelated series of three components: (1) the chemical signal itself, (2) the anatomy involved in perception, and (3) any behavioral or physiological response (Fig. 3.10). Each component can impact the next or previous step, and each is subject to evolutionary history as well as natural and/or sexual selection.

The conceptual model in Fig. 3.10 provides a general framework that is applicable to most any signaling system and has helped guide my own research on the Crested auklet (*Aethia cristatella*). Earlier in this chapter I discussed the particulars of avian odor, such as the production and chemistry of odor signals (see 3.3). I also discussed behavioral responses to odor signals (see 3.4). I will now examine the remaining component of the model, sensory perception, as it relates to avian olfactory anatomy. This final component is critical, as an understanding of chemoreception is central to studies of odor signals in birds.

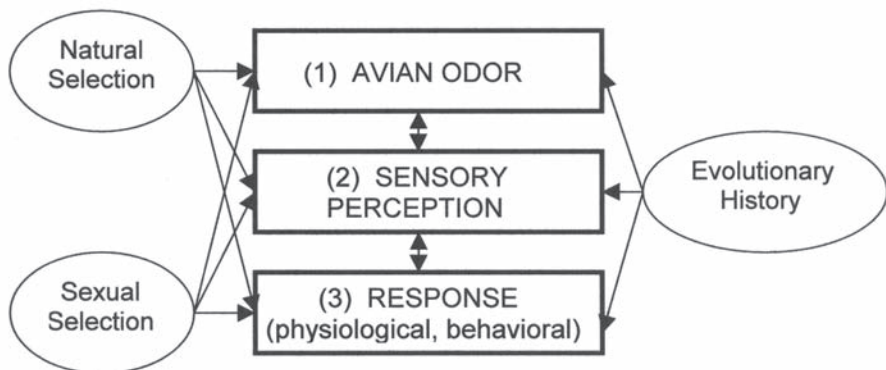


Fig. 3.10 A conceptual model for the study of avian odors. Chemical communication, like any signaling system, is divided into three basic components: (1) odor chemistry of the signal itself, (2) anatomy involved in perceiving the signal, and (3) the resulting behavioral or physiological response. Each component is subject to natural and sexual selection as well as evolutionary history. Original.

3.7 AVIAN OLFACTION: STRUCTURE AND FUNCTION

Though I provide a brief overview of anatomy, readers are encouraged to refer to more detailed material (Bang 1971; Bang and Wenzel 1985; Roper 1999). Chemical perception of vertebrates is divided into three senses: (1) the olfactory system, in which volatile chemical information is detected by olfactory receptors, (2) taste or gustation, in which compounds are detected by receptors in the buccal cavity, and (3) the trigeminal system, which perceives nociceptive stimuli, such as the burning sensation of a chemical irritant (Roper 1999). Most studies of birds do not distinguish between the three systems, although birds exhibit tastebuds and a sense of taste (e.g. Wenzel 1973, Ganchrow and Ganchrow 1985) as well as trigeminal responses (e.g. Mora *et al.* 2004; McKeegan *et al.* 2005; reviewed in Roper 1999). However, birds appear to lack a vomeronasal organ and an accessory olfactory bulb, features associated with the detection and processing of some types of chemical signals in other organisms (Riecke and Wenzel 1975, 1978). For simplicity, like Roper (1999), I consider “olfaction” to include any means by which volatile chemosensory information is obtained by a bird. It may involve one or more of the systems mentioned above.

Once air enters a bird’s nares, it passes through a series of three chambers, arranged in sequence, which contain mucous-covered invaginations of cartilage and/or thin bone called conchae (Fig. 3.11). As air flows caudally through each chamber, it is probably cleaned, warmed and moistened by the anterior and maxillary conchae. Odors are detected upon reaching the olfactory concha in the third chamber. Olfactory conchae are covered in a layer of sensory cells called the olfactory epithelium (Fig. 3.12). The epithelium is similar to that of other vertebrates, as it is densely packed with olfactory

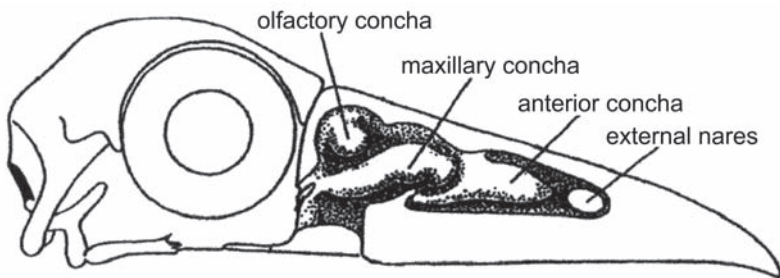


Fig. 3.11 A longitudinal section through a generalized bird beak illustrating the conchae (invaginated or convoluted structures) found in the three chambers of the nasal cavity. Air enters through the external naris, then passes over the anterior concha in the first chamber, and the maxillary concha in the second chamber. Odors are detected in the olfactory concha (OC) in the third chamber. Generalized drawing adapted from Roper, T. J. 1999. Pp. 247–332. In P. J. B. Slater, J. S. Rosenblat, C. T. Snowden and T. J. Roper (eds), *Advances in the Study of Behavior*, Vol. 28. Academic Press, Boston, Fig. 1.

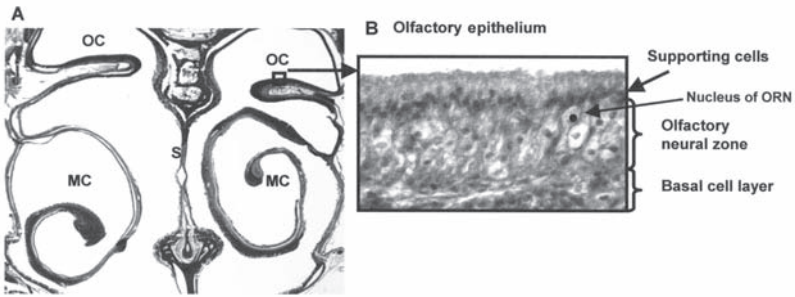


Fig. 3.12 **A.** Transverse section through the nasal cavity of an adult crested auklet (*Aethia cristatella*). The olfactory conchae (OC) of this species are fairly small, finger-like structures. This photo was taken in an anterior region of the third nasal chamber where the OC project dorsally to maxillary conchae (MC). The septum (S) is also shown. **B.** Close-up (40 × objective) of cell layers in the olfactory epithelium. Nuclei of olfactory receptor neurons (ORN) are visible within the olfactory neural zone. Other cell layers of the epithelium are also indicated. Original.

receptor neurons (that contain chemoreceptors) and other specialized cells (Fig. 3.12; Wenzel 1973, 1987). Olfactory receptor neurons transmit information via the olfactory nerve to the olfactory bulb, a discrete structure in the anterior region of the brain, for further processing (Pearson 1972; Wenzel 1987).

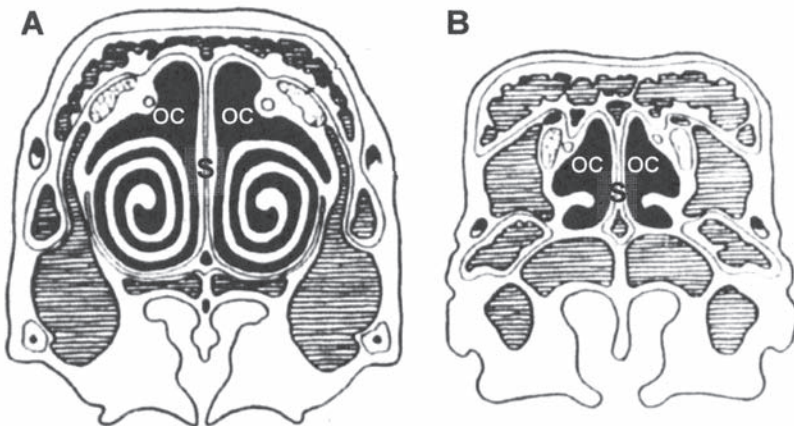


Fig. 3.13 Transverse section of the olfactory conchae of **(A)** the turkey vulture (*Cathartes aura*), a species well-known for its olfactory abilities, and **(B)** the black vulture (*Coragyps atratus*), a species that emphasizes visual cues, rather than olfaction. Drawing shows striking differences in surface area (scrolling) of the olfactory conchae (OC), which are covered in olfactory receptor epithelium. S=septum. (Unlike Fig. 3.13, this drawing was made in the caudal end of the third nasal chamber where maxillary conchae are not visible). Adapted from Bang, B. G. 1971. *Acta Anatomica Supplementum* 58 (79): 1-71, Fig. 16.

3.7.1 Form and Function of Olfactory Anatomy

The gross olfactory anatomy of birds is quite variable and has been described for close to 200 species from 23 Orders (Bang and Cobb 1968; Bang 1971). Form can be predictive of function in several ways. First, extensive surface area (scrolling) of olfactory conchae occurs in birds that are known to rely on smell during foraging (Fig. 3.13), such as the Turkey vulture (*Cathartes aura*; Stager 1964; Bang 1971), the Brown kiwi (*Apteryx australis*; Wenzel 1968), and the Northern fulmar (*Fulmaris glacialis*; Wenzel and Meisami 1990). Second, across avian orders, increased size of the olfactory bulb relative to brain size, a measure known as the “olfactory bulb ratio,” correlates with greater olfactory acuity (Table 3.3; Clark *et al.* 1993). Third, within families, larger bulbs correlate with nocturnal behavior, a habit that likely emphasizes olfactory adaptation (Healy and Guilford 1990). Larger olfactory bulb size may indicate greater functional capacity, because it probably reflects an increase in the number of cells and neural circuits contained within (Table 3.3; Meisami 1991).

Table 3.3 Olfactory bulb, brain hemisphere size and olfactory bulb ratio (OBR) for four birds with large olfactory anatomy (highlighted in bold), a diving petrel, non-passerines and passerines (mean $\pm$ sd), and the European starling

Common name	Species	Bulb diameter (mm)	Hemisphere diameter (mm)	Olfactory bulb ratio (%)
Snow Petrel^{a,b}	<i>Pagodroma nivea</i>	6.7	18.0	37.0
Brown Kiwi^{a,c}	<i>Apteryx australis</i>	12.0	35.0	34.0
Kakapo^d	<i>Strigops habroptilus</i>	10.2	33.8	30.2
Turkey Vulture^{a,e}	<i>Cathartes aura</i>	6.0	24.0	28.7
Diving Petrel ^f	<i>Pelecanoides georgicus</i>	2.0	11.3	18.0
Non-passerines ^f	<i>n</i> = 81 species	3.4 $\pm$ 1.9	17.1 $\pm$ 5.9	19.6 $\pm$ 6.5
Passerines ^a	<i>n</i> = 25 species	1.5 $\pm$ 0.5	13.6 $\pm$ 0.2	9.7 $\pm$ 4.9
European Starling ^a	<i>Sturnus vulgaris</i>	1.4	14.5	9.7

^a From Bang and Cobb (1968)
^b Largest olfactory bulb ratio reported for any bird (Bang and Wenzel 1985)
^c For olfactory behavior, see Wenzel (1968)
^d From Hagelin (2004)
^e For olfactory behavior, see Stager (1964)
^f For olfactory behavior, see Bonadonna *et al.* (2003a)
^g Values calculated 80 non-passerines from Bang and Cobb (1968), plus the Kakapo (Hagelin 2004)

While larger olfactory anatomy in birds appears to correlate positively with function in some species, the reverse is not necessarily true. For example, European starlings (*Sturnus vulgaris*), Crested auklets (*Aethia cristatella*) and Diving petrels (*Pelecanoides* spp.) are all capable of employing odors during the breeding season (Clark and Mason 1985; Bonadonna *et al.* 2003a; Hagelin

et al. 2003). Yet, each has fairly small olfactory anatomy (Table 3.3 for *S. vulgaris* and *Pelecanoides*; Fig. 3.12 for olfactory conchae of *A. cristatella*). Consequently, even small anatomical structures are quite capable of detecting certain odors. The larger olfactory anatomy of some birds (Table 3.3) may reflect an ability to detect a greater variety of odors (Adrian 1951 as cited in Bang and Wenzel 1985), but this idea remains untested.

3.7.2 Olfactory Microstructure

Data on the microstructure of the avian olfactory system are scarce. Our laboratory examined how the microstructure of the tangerine-scented Crested auklet (*Aethia cristatella*) compared to four other auklet species (all but one of which lacked plumage odor and the unique nape-sniffing display behavior; see 3.4.5, Displays of crested auklets). Contrary to expectation, *A. cristatella* did not exhibit more olfactory epithelium than expected for its body size (Fig. 3.14). In fact, *A. cristatella* did not differ dramatically from any auklet species with regard to any aspect of olfactory anatomy that we measured (Fig. 3.15). We obtained a similar pattern for the whiskered auklet (*Aethia pygmaea*; Figs. 3.14, 3.15A), the only other species that produces both an unusual plumage odor (Douglas *et al.* 2005a) and exhibits a nape-sniffing display identical to *A. cristatella* (I. L. Jones, personal communication). If *A. cristatella* (and possibly *A. pygmaea*) employ social chemosignals with relatively unremarkable olfactory microstructure, the pattern may apply more broadly to other birds.

Olfactory bulb. Descriptive accounts of the laminar layers of cells within the olfactory bulb of the brain suggest that birds are similar to reptiles, in that they lack some of the distinctive layering patterns found in mammals (Allison

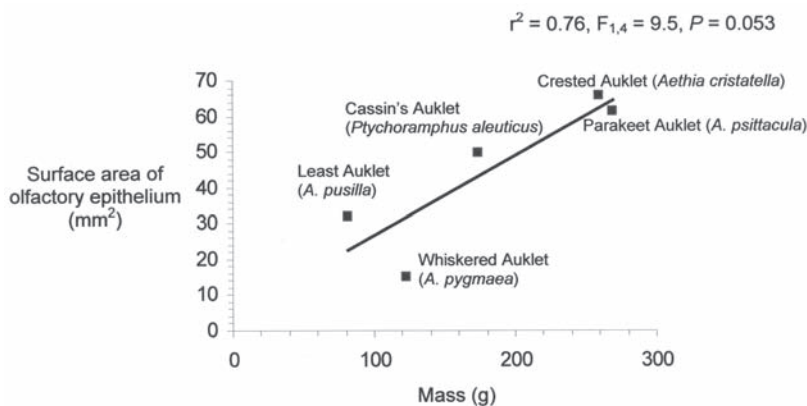


Fig. 3.14 The amount of olfactory epithelium scales positively with body size across five auklet species. Interestingly, the Crested auklet (*Aethia cristatella*) does not appear to exhibit more olfactory epithelium than expected for its body size. Data represent mean values ($n=3$ [*A. cristatella*] and 2 of each other species). Serial sections of olfactory tissue were measured according to methods in Meisami (1989).

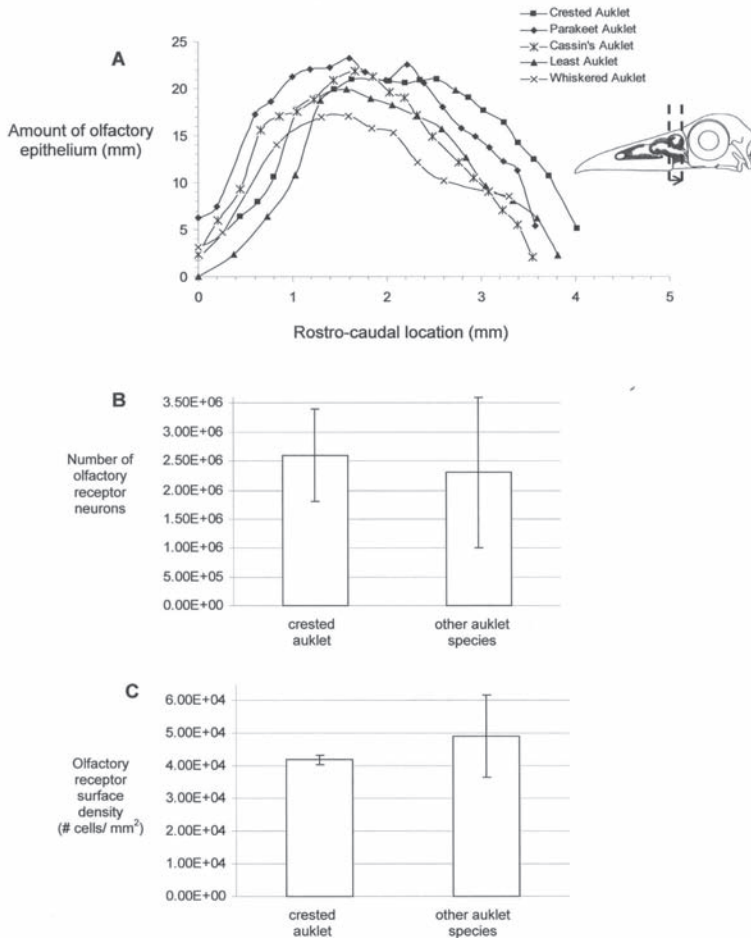


Fig. 3.15 The distribution of olfactory receptor tissue along a longitudinal transect of the olfactory conchae was quite similar between auklet species (**A**)^{†,‡}. Likewise, the total number of olfactory receptor neurons (**B**)^{*} and the density of receptor neurons per mm² of olfactory epithelium (**C**)^{*} did not differ between the Crested auklet (*Aethia cristatella*) and four other auklet species. Methods followed Meisami (1989) and Paternostro and Meisami (1993).

^{*}Data represent means and standard deviations of the specimens presented in Fig. 3.14.

[†]Drawing in **A**. indicates the region of the transect. Data were collected from transverse serial sections (10 μ m) that began at the first dashed line and proceeded caudally, through the olfactory conchae, to the second dashed line.

[‡]The longitudinal transects provide a relative comparison of different auklet species. The first data point of each line represents the point at which olfactory receptor tissue was first noted in a 10 μ m section. Serial sections were quantified approximately every 0.4 mm thereafter.

1953; Andres 1970). In particular, the glomerular layer, the region where the axons of olfactory receptor neurons converge into the brain, appears to be relatively undifferentiated in birds (Wenzel and Meisami 1990). Yet, we know very little else. The cells of the olfactory bulb have been quantified in two Rock doves (*Columba livia*) and one Northern fulmar (*Fulmar glacialis*; Wenzel and Meisami 1987, 1990). In both species, mitral cells, structures that process olfactory signals, were counted. In *F. glacialis* only, two other cell types were also measured; glomeruli, sites where the axons of chemoreceptors converge, and granular cells, the innermost relay cells to the brain. While the number of cells in both species compared favorably to mammals, interspecific comparison indicated the relationship between bulb size and mitral cell number was more complex than expected (Wenzel and Meisami 1987), possibly because the specimens belonged to very different avian orders. Electrophysiological recordings have been made in numerous avian species from multiple structures in the olfactory system (reviewed in Roper 1999). Those from single olfactory bulb neurons in the Domestic chicken (*Gallus domesticus*) verify that cells exhibit adaptation in response to prolonged odor exposure (McKeegan and Lippens 2003).

3.7.3 Gaps in Anatomical Studies

Studies that quantify the microstructure of the avian olfactory system are few. Such data are key to understanding how chemosensory adaptations evolve in birds, their relevant ecological contexts, and any structural or seasonal changes associated with taxa that employ odor cues. Investigations that consider phylogeny are also rare, with the exception of Healy and Guilford (1990). Most studies examine only 1-3 individuals per species, making it difficult to interpret among-taxa comparisons with confidence.

Studies that focus on seasonal change could yield predictive tools for identifying promising species for future behavioral studies of odor use. For example, seasonal shifts in olfactory acuity occur in European starlings (*Sturnus vulgaris*; Clark and Smeranski 1990) and have been implicated in the selection of nest materials (see 3.2.1). However, any underlying structural changes that may occur, like those of other vertebrates (e.g. Dawley *et al.* 2000), are not well understood.

Development. Studies of the domestic chicken (*Gallus domesticus*) have provided interesting insight into the development of the avian olfactory system (e.g. Drapkin and Silverman 1999; reviewed in Ayer-LeLievre *et al.* 1995; Roper 1999). Details of developmental and functional properties of the olfactory receptor epithelium have also been examined (Fornaro *et al.* 2001; Lalloue *et al.* 2003; Comte *et al.* 2004; Jung *et al.* 2005). However, to the best of my knowledge, studies quantifying the macro- and microstructure of the nasal cavity and olfactory bulb of a developing chick are needed. Wenzel and Meisami (1990), for example, reported that the surface area of olfactory epithelium from one fulmar chick (*Fulmar glacialis*) was considerably less than

that of an adult. The olfactory bulb ratio (see 3.7.1) of Blue petrel chicks (*Halobaena caerulea*) is also smaller than that of an adult, but by the time a chick fledges, it is similar to adult-sized (G. Cunningham, pers. comm.). Yet, we know little else about developmental changes in the extent of olfactory epithelium, receptor cell density, or odor processing capacity of the brain, like we do in mammals (e.g. Meisami 1989; Rosselli-Austin and Williams 1990; Apfelbach *et al.* 1991). Changes in the olfactory structure of vertebrates usually coincide with changes in function, such as modifications that occur during odor "imprinting" (e.g. Rehn *et al.* 1986; Jarrard, 1997). Consequently, our understanding of birds would greatly benefit from a detailed study of olfactory structure in a developmental series of an avian model species, such as *G. domesticus*. Such data would serve as a useful comparison for other avian groups, such as seabirds, in which adaptive responses to body or environmental odors are emphasized (see 3.4).

3.8 CONCLUSIONS

Odors and chemical perception provide a unique and largely overlooked modality, which, in addition to sight and sound, apply to studies of avian reproductive behavior. Combined, the evidence indicates: (1) Both the production of scent and the response to environmental odors is widespread in birds. (2) Odors are linked to a variety of social situations during reproduction, all of which involve adaptive behavioral responses, such as: (a) nest building, (b) homing to nest sites or breeding areas, (c) discrimination between mates and conspecifics, (d) courtship and sexual selection, and (e) development, odor learning, and parental care. (3) Given the broad range of circumstances that implicate avian-derived odors, scent has the potential to alter how we interpret reproductive and social behavior in a wide variety of bird species, and may even be applicable to situations involving species recovery. (4) Research thus far has tended to focus on arbitrary situations and isolated cases; we have yet to obtain a general understanding of how odors impact avian breeding behavior or reproduction. (5) Future, interdisciplinary studies that explore avian odor chemistry, anatomy and behavioral responses hold great promise, particularly those that compare avian scent to well-documented chemosensory mechanisms that function in the reproduction and development of other vertebrate systems, such as mammals and fish.

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Sexual Dimorphism

Ian R. Hartley

4.1 INTRODUCTION

Differences between the sexes have long been a source of fascination for people. This is especially true for ornithologists because birds have provided many of the model examples for the evolution of sex differences in body form and behavior. Charles Darwin devoted several chapters to birds in his '*Descent of Man and Selection in Relation to Sex*' (Darwin 1871), and considered them to be more important for their diverse secondary sexual characters than any other taxonomic group. Darwin referred to such species as the Peacock (*Pavo cristatus*) with its elaborate male plumage and long trains used in display, the Brown songlark (*Cincloramphus cruralis*), where males appear similar in plumage to females but are much larger in size, and the Ruff (*Philomachus pugnax*), where males are both larger than females and have elaborate breeding plumage (Darwin 1871).

Historically, variation in the extent and types of sexual dimorphism have been explained in relation to the mating system and pattern of parental care (reviewed in Andersson 1994). For example, in polygyny, males that are larger or have more elaborate ornamentation have greater success at competing for, or attracting, females and so large size or plumage elaboration become traits that are favored through sexual selection. On the other hand, differences in parental care effort between the sexes might lead to the sex that provides most care being under natural selection pressure to reduce predation risk by being cryptic. There are, however, problems with these explanations because an uncomfortably large number of species do not fit the patterns. In the Chaffinch (*Fringilla coelebs*) and House finch (*Carpodacus mexicanus*), for example, males are brightly colored while females are dull, yet both species breed in monogamous pairs, with both sexes provisioning the nestlings. In Blue tits (*Cyanistes caeruleus*) the sexes appear similar to our eyes (but see Eaton 2005 and Chapter 1) and both are brightly colored, despite an apparently monogamous and biparental life history. The aim of this chapter is to discuss

the roles of sexual and natural selection in the evolution of sexual dimorphism in birds, and to highlight the different evolutionary pathways that can lead to size and color differences between the sexes.

4.2 SEX DIFFERENCES IN NATURAL AND SEXUAL SELECTION

Sexual differences in traits such as plumage color or ornaments, body size, or the presence of weapons (e.g. spurs), have evolved because males and females are under different selection pressures; either from natural selection or sexual selection (Darwin 1871). The components of the life histories of the sexes usually differ to some degree, most obviously in sex biases in the parental care roles but other differences also occur. For example, there are differences between the sexes in migration strategies in European blackbirds (*Turdus merula*) (Schwabl 1983), in foraging behavior in Northern gannets (*Morus bassanus*) (Lewis *et al.* 2002), in foraging niche in the Green woodhoopoe (*Phoeniculus purpureus*) (Radford and Du Plessis 2003), Northern giant petrels (*Macronectes halli*) (Gonzalez-Solis 2004) and Huia (*Heteralocha acutirostris*) (the extinct Hawaiian species; Darwin 1871) where the sexes differ markedly in bill morphology, and sex differences in parasite burdens are common across many species (Poulin 1996). Such differences are ultimately often associated with reproductive strategies and are mechanistically inter-linked but natural selection could influence the sexes in different ways, which can lead to sexual dimorphism.

Sexual selection also acts upon males and females in different ways. Sexual selection is reviewed in chapters 1, 2 and 5 but can briefly be described as the process which arises from differences in reproductive success caused by competition for mating opportunities (Darwin 1871; Andersson 1994). Here, we are not directly interested in sex differences in primary sexual characteristics, such as the ability to produce and transfer sperm, or lay a viable egg. We are more concerned with secondary sexual characteristics; traits that confer some mating advantage because they are preferred by the opposite sex, or they enable success in competitions over matings. In general, one sex (usually the female) limits the reproductive rate of the other (usually the male), either because eggs are large and costly items to produce relative to sperm, or because the needs of parental care limit the rate at which the slower sex can reproduce, which skews the operational sex ratio (Clutton-Brock and Vincent 1991; Clutton-Brock and Parker 1992). Although there are exceptions, it is usually the males which compete for the females, as they are the resource which limits male reproductive rate (Bateman 1948). The competitive sex is the one under the greater sexual selection pressure, and so it is most often male birds that have the most elaborate or colorful plumage, spurs, or colorful wattles because these are traits which enhance reproductive success through mate choice or competition. The evolution of differences in body size could also be under sexual selection if large males out-compete smaller males but it could equally be the result of body size selection processes on females.

Ultimately, the combination of sex differences in natural and sexual selection will lead to potentially different outcomes in terms of the morphology or behavior of the two sexes.

For most traits, there are genetic correlations between the characteristics of males and females but selection may act on only one sex. In this case, it is possible that sexual selection acting on the trait in the males might indirectly lead to the development of the same trait in females. If females suffer great costs in possessing such traits it is likely that their expression will eventually become sex-limited (to males only), either through the gene becoming sex-limited, or through a secondary mechanism which controls whether or not it is expressed (Cuervo and Møller 2000). If the costs to females of having male secondary sexual traits are very low, however, it might lead to a situation where both sexes are bright or have ornamentation, although in such cases the males usually tend to be brighter or have larger ornaments despite the overall similarity between the sexes. In some species, there is evidence of mutual mate choice based on similar secondary sexual characteristics in both sexes (Jones and Hunter 1993) and in those cases we might predict that selection would favor sexual monomorphism rather than dimorphism.

4.3 COLOR DIMORPHISM

4.3.1 The Evolution of Sexual Color Dimorphism

The evolution of brightly colored plumage is usually associated with intra-sexual selection, where mating success is determined by the likelihood of being chosen for matings by the opposite sex and the number of females that are attracted, rather than through contests between members of the same sex; the peacock is the classic example (Petrie *et al.* 1990, 1992; Petrie and Halliday 1994) (Fig. 4.1A). There are, however, many apparent exceptions to the relationship between polygyny and the extent of color dimorphism across species. Examples of species that show sexual color dimorphism, yet are monogamous, include Chaffinch, Zebra finch (*Taeniopygia guttata*) (Fig. 4.1B,C), House finch, Yellowhammer (*Emberiza citrinella*), Red cardinal (*Cardinalis cardinalis*) and Indigo bunting (*Passerina cyanea*) (Owens and Hartley 1998). One possible explanation for the many anomalous species that are color dimorphic but apparently monogamous is that sexual selection can still act, even in monogamy, when there is variation in quality between individuals in relation to their reproductive ability. For example, there may be selection on individuals that are attractive to the opposite sex if that allows them to breed earlier and early breeders are more likely to successfully rear a second brood. Another explanation is that the apparently monogamous species have been classified to the wrong mating system. Following the discovery that DNA fingerprinting could be used to assign accurate parentage in birds (Burke and Bruford 1987; Wetton *et al.* 1987), and the subsequent development of other molecular techniques, there have been many studies that have demonstrated that the social mating system of birds does not necessarily



Fig. 4.1 **A.** The Peacock is one of the classic examples of sexual dimorphism. Sexual dimorphism based on iridescent blue plumage is frequently associated with sexual displays and extra-pair mate choice in birds. **B.** Female and **C.** Male Zebra finches. These finches are sexually dimorphic; males have black breast bands, orange cheek patches and chestnut flanks. The use of carotenoid-based colors in sexual signaling could provide females with accurate information on the quality of the male. Photos: Ian Hartley.



reflect the genetic mating system. There are many species where the social mating system, as witnessed by directly observing the birds during the breeding season, is best described as monogamous but the genetic mating system, as revealed by DNA analysis, is polygynous or often polygynandrous. Females of some species seek extra-pair copulations with males outside the monogamous bond, and these can lead to mixed paternity within broods (genetic polyandry) as well as a skewing reproductive success within males (genetic polygyny). The incidence, causes and consequences of extra-pair paternity are reviewed more fully in Chapter 8 but the important aspect for our understanding of sexual dimorphism is that there is potential for mate choice for extra-pair fertilizations to lead to a greater than expected sexual selection in socially monogamous species. It is possible that the incidence of extra-pair paternity has had a significant influence on the evolution of sexual dimorphism. A comparative analysis across bird species found support for the idea by showing a correlation between the extent of extra-pair paternity and the degree of sexual dimorphism for plumage brightness (Møller and Birkhead 1994). Ian Owens and I took the comparative analysis a stage further using a dataset that included 73 bird species for which there was an accurate estimate of the incidence of extra-pair paternity (Owens and Hartley 1998). Controlling for the effects of any phylogenetic relationships, we carried out an analysis that included both color and size dimorphism, skews in parental care effort and different forms of plumage color dimorphism. The analysis clearly showed that different variables were related to the two forms of sexual dimorphism: body size and plumage color (Table 4.1). Sexual dimorphism for body size is discussed further below, but was most related to the social mating system, as described by watching the birds in the field, without additional

Table 4.1 Associations between sexual dimorphism for a) size and b) plumage color, and various indices of social, sexual and parental behavior. The analyses control for the effects of phylogeny and are based on independent contrast scores resulting from CAIC analysis (Purvis and Rambaut 1995). Values of τ refer to two-tailed Kendall rank-order correlation coefficient tests of the null hypothesis that changes in dimorphism are not associated with changes in the independent variable (from Owens and Hartley 1998).

<i>Independent variable</i>	<i>(a) Size dimorphism (n = 26)</i>		<i>(b) Plumage-color dimorphism (n = 19)</i>	
	τ	<i>p value</i>	τ	<i>p value</i>
female weight	-0.10	>0.25	—	—
mating system	0.37	<0.01	0.19	>0.25
frequency of extra-bond young	-0.09	>0.50	0.45	<0.01
frequency of extra-bond broods	-0.10	>0.25	0.40	<0.01
sex bias in incubation	-0.01	>0.90	-0.04	>0.75
sex bias in brood provisioning	0.30	<0.05	0.03	>0.75
sex bias in passive brood defense	0.05	>0.50	0.17	>0.25
sex bias in active brood defense	0.27	<0.05	0.22	>0.10

data on parentage. Sexual dimorphism for plumage color was strongly and positively correlated with the incidence of extra pair paternity but not social mating system, so species which had the greatest sexual dimorphism for color tended also to be those species where extra-pair paternity was most common.

The differences we found between color and size dimorphism suggest that the two forms of dimorphism are the result of different selection pressures. The analysis suggests that mate choice (inter-sexual selection), but not competition between members of the same sex (intra-sexual selection), is important in determining the evolution of sexual differences in plumage color. There are a number of studies that provide evidence for female choice of males during extra-pair encounters being based on plumage variation. For example, female Barn swallows (*Hirundo rustica*) prefer longer tailed males for extra-pair partners (Saino *et al.* 1997); the white forehead and wing patches on male Collared flycatchers (*Ficedula albicollis*) have been shown to be preferred by females via extra-pair mate choice (Sheldon and Ellegren 1999); and female Yellowhammers seeking extra-pair matings prefer males that are more yellow (Sundberg and Dixon 1996). Although sexual selection through extra-pair mate choice is likely to be an important contributor to the evolution of sexual dimorphism in monogamous species, it is not necessarily the only selection force. In the monogamous House finch, for example, males with redder plumage are preferred by females, yet the incidence of extra-pair paternity is not related to male redness in this species (Hill *et al.* 1994). Instead, a strongly male biased population sex ratio, combined with asynchronous breeding by females, leads to a heavily male biased operational sex ratio and so strong sexual selection through a different route. Overall, then, the evolution of sexual color dimorphism in birds is strongly related to sexual selection through overt female choice, and cryptic female choice, via extra-pair copulations, is an important contributing factor (Owens and Hartley 1998; but see also Dunn *et al.* (2001) who suggest we have over-emphasized the importance of extra-pair mate choice).

An alternative hypothesis proposed to explain color dimorphism in birds is that the need to avoid hybridization results in striking male plumages to aid species recognition by females (Wallace 1889; Lack 1968). This hypothesis was widely supported until relatively recently but the emphasis has now shifted towards sexual selection within species being the driving force for color dimorphism (Bennett and Owens 2002). There are three main lines of argument for rejecting the importance of species recognition in the evolution of color dimorphism. First, a comparative analysis compared color dimorphism between species which either had geographically similar (sympatric) or separate (allopatric) ranges, with the prediction that hybridization risk was greater in the sympatric zone. When hybridization risk is high, the species recognition hypothesis predicts that dimorphism should be more common, but when controlling for the potentially confounding effects of phylogeny, the analysis showed that this was not the case (McNaught and Owens 2002). Second, if dimorphism has evolved due to the needs for species

recognition, the plumage that acts as the specific signal should be less variable between individuals than the plumage parts that are not involved in the identification of species. This was not the case, however, and both hue and brightness of colors were no differently variable between regions of the plumage used in sexual displays, versus those not used in such displays (McNaught and Owens 2002). Third, there tend to be fewer species on islands than on mainland regions, so the risk of hybridization is lower on islands. The species recognition hypothesis would predict, therefore, that island species are less likely to be sexually color dimorphic than mainland species. A comparative analysis across 46 pairs of species which had an island and a mainland form showed that island species were not significantly less dimorphic than expected by chance (Owens and Clegg 1999). So, overall, there is compelling evidence against species recognition being the driving force for the evolution of color dimorphism in birds, and a growing body of evidence supporting a strong role for sexual selection.

4.3.2 The Hormonal and Genetic Basis for Plumage Dimorphism

Whether a bird has male or female plumage can be determined by two factors: the hormonal state of the individual and the presence of sex-linked genes controlling plumage type. The male hormone, testosterone, is produced in the testes of males and its effects can be experimentally explored using a combination of vasectomy and testosterone injection. Similarly for females, estrogen is produced in the ovaries and can be manipulated by ovariectomy and injection of estrogen. Dimorphic plumage traits that do not change in response to hormone manipulation are most likely to be controlled by sex-linked genes.

Many traits associated with males are controlled by testosterone, for example, the development of spurs, wattles, bill pigmentation, aggression and territorial behavior (Wingfield *et al.* 1990; Owens and Short 1995; Roberts *et al.* 2004). In species which have a prenuptial moult, from winter to breeding plumage, there is a simultaneous rise in the circulating testosterone levels as a result of the annual development of the testis. This does not, however, mean that testosterone is the cause of the development of male plumage. In the absence of testosterone males of many species develop normal male plumage but females deprived of estrogen also develop male plumage. So, in many species, the default state is the bright male plumage, which is 'switched off' by the presence of circulating estrogen (Owens and Short 1995). This explains why some female birds, such as peacocks, occasionally seem to change sex later in life, especially after an infection affecting the ovaries. It is usually a consequence of a fall in the estrogen which was inhibiting the expression of male plumage (Owens and Short 1995). Despite this general pattern, there are some species where testosterone does seem to control differences in plumage expression between the sexes, for example in Ruff (Lozano and Lank 2004) where variation in male lekking behavior is strongly correlated with plumage type (van Rhijn 1983; Widemo 1998a, b).

In species that do not have a prenuptial molt but instead moult annually after breeding, sex differences in plumage seem to be under genetic control (Owens and Short 1995). In House sparrows (*Passer domesticus*), for example, the black throat patch of the male is a plumage signal that has evolved under sexual selection (Møller 1988; Vaclav *et al.* 2002; but see Whitekiller *et al.* 2000), and neither estrogen nor testosterone manipulation influence the overall presence of male or female plumage type in this species (Owens and Short 1995). Despite that, however, plumage variation between individual males has been shown to be affected by testosterone; males with experimentally elevated testosterone developed larger areas of black on their throats (Evans *et al.* 2000). So it seems that while the presence or absence of male plumage is not under hormonal control in species like the house sparrow, hormones do control the size of plumage traits, which could potentially influence mating success (Roberts *et al.* 2004). The link between testosterone and sexual signals is mainly of interest because of the additional role testosterone might play in depressing the immune system. The interaction of the hormones, plumage signal and immune function of individuals has been suggested as way in which honest signals of quality might have evolved through mate choice (Folstad and Karter 1992). Currently, our understanding of the interactions is rather poor so it would be a useful area for further research (Roberts *et al.* 2004).

4.3.3 How Should We See Color?

Humans and birds see the world in different ways. While humans see colors via the red, green and blue detecting cones in the retina, birds have a fourth cone type which detects ultraviolet light. So, when trying to understand the evolution of color variation in birds, it is important to take into account how the birds see each other (Bennett *et al.* 1994; Cuthill *et al.* 2000). There are a number of species that look nearly sexually monomorphic to human eyes yet, viewed from the perspective of a bird, they are strongly dimorphic. For example, the majority of Blue tit males and females are not easy to distinguish in the field; although males are often a touch brighter, there is much overlap between the sexes. When viewed through eyes with ultraviolet vision, however, blue tits are strongly sexually dimorphic. Using a color reflectance spectrometer, Andersson *et al.* (1998) quantified the light wavelengths reflected from blue tit plumage and showed that the crown feathers of males and females differed most in the 370 nm region (outside the human range, which is generally 400–700 nm). Since then, several studies on blue tits have demonstrated that the ultraviolet component of male plumage is important in sexual signaling (Hunt *et al.* 1999; Sheldon *et al.* 1999; Delhey *et al.* 2003; Griffith *et al.* 2003) (see also Chapter 1).

Sexual signals based on ultraviolet plumage have also been found in other species where previously we assumed the sexes were similar in color (Bennett *et al.* 1997), or where we underestimated the extent of sexual plumage dimorphism (Bennett *et al.* 1996). It is likely that, as more data become

available, we will need to incorporate the ultraviolet component of bird plumages into our analyses of sexual plumage dimorphism.

As well as appreciating how color is seen through different type of eyes, it is also important to consider the light environment in which the colors are perceived, for example, plumage that shows up well under the green light found below a forest canopy might appear cryptic in an open environment. So, whether we are interested in understanding camouflage or signals, we need to know the environmental light conditions in which the plumage is used (Endler 1993). In a comparative analysis across 20 pairs of species, where one species lived in open habitat and the other lived in closed habitat, McNaught and Owens (2002), found that the variation in color between species was best explained by the light environment of the habitats they occupied. Consistent with the predictions of the light environment hypothesis, they found that species which used closed habitats tended to have more red and orange in their plumage, especially on those regions of the body used in displays; red colors stand out more in green light environments. Species of more open habitats tended to have more reflective (brighter) plumages, and showed no patterns in relation to chroma (color) (McNaught and Owens 2002). Therefore, we need to consider not just the color of plumage but the viewing environment and the recipient of plumage signals when trying to explain the evolution of color differences between the sexes, or indeed its variation within a sex.

4.3.4 Types of Color

The coloration of feathers depends on pigments, which absorb light of particular wavelengths, and the microstructure, which reflects and scatters light in ways which produce color (Voitkevich 1966). In feathers the two main classes of pigments are melanins, which produce black and brown colors, and carotenoids, which produce bright yellow, orange and red colors (see Chapter 2). In combination with melanins, carotenoids can produce green feathers, and when carotenoids are combined with some proteins they can form purple feathers (Goodwin 1984). Structural colors are generated from the way light is scattered or diffracted by the microstructure of the feather, and these tend to be whites, blues and iridescent colors (see Chapter 2 for a fuller discussion). As we were interested in trying to understand the variation in types of colors that birds use in their plumage, Ian Owens and I included the type of color in our comparative analysis of sexual dimorphism and extra-pair paternity (Owens and Hartley 1998). We divided the colors into those based on three components: melanins, carotenoids, and structural colors. Our analysis suggested that classifying birds as either dimorphic, or not, was probably too simplistic, because the type of color dimorphism was also important. We found that the strong relationship between overall plumage dimorphism and extra-pair matings was mainly due to structural colors, and that melanin-based dimorphism was mostly associated with the extent of the bias towards one sex providing most parental care. In a further analysis of plumage colors

in parrots, Hausmann *et al.* (2003) found a strong relationship between plumage with structural coloration, especially ultraviolet and fluorescent colors, and their use in sexual courtship displays. Furthermore, ultraviolet and fluorescent color patches were positioned so as to maximize contrast and so enhance the signal (Arnold *et al.* 2002; Hausmann *et al.* 2003), in the way that you might place an object on a contrasting colored background to make it stand out more (see Hasson 1991).

The variation in the use of different types of color is not yet well understood but there are some suggestions as to why the different color systems might be important. Carotenoids are compounds that cannot be physiologically synthesized by birds but which must be ingested as part of their diet (Olson and Owens 1998). One suggestion is that the compounds are relatively rare in the environment, so are costly for the birds to accumulate and therefore provide an honest signal to potential mates about the foraging, or other, abilities of the bird. They have also been implicated as being important for immune system function (e.g. Saino *et al.* 1999; Horak *et al.* 2001; Blount *et al.* 2003; Saks *et al.* 2003), so shunting carotenoids into physiologically inaccessible tissues such as feathers might incur costs. If they provide costly, honest signals of quality, it makes sense that they could be used by discriminating potential mates (Olson and Owens 1998). Melanins differ from carotenoids in that they can be synthesized by birds for use as pigments, and for this reason it has been suggested that they are relatively cheap to produce and use as plumage signals (Maynard Smith and Harper 1988), although the evidence for this assumption is lacking. It is possible, however, that melanins might be similar to carotenoids in that they are costly to use as plumage pigments, because the immune system shares some necessary amino acids with the pathway that produces melanin (Owens and Wilson 1999). Other evidence, from a comparative analysis within the cardueline finches, suggests that plumage based on carotenoid coloration is more often associated with sexual color dimorphism than is melanin-based coloration (Badyaev and Hill 2000). This leads to the suggestion that the two forms of color source are under different selection pressures and provide potential sexual partners with different information. Despite that, we still do not know why some species exhibit sexual dimorphism with plumage based on melanin (e.g. house sparrows), whereas others use carotenoids (e.g. house finches). Furthermore, signals using carotenoid colors in house finches vary in color intensity and size independently and are under different selection pressures, which vary further between populations (Badyaev *et al.* 2001), suggesting that the variation in coloration in relation to sexual signaling is potentially much more complex than we originally thought.

4.4 SIZE DIMORPHISM

Sexual size dimorphism is where one sex is larger than the other. The scale of size dimorphism extends all the way from the sexes being virtually identical in size, as in the Silver-eyes (*Zosteropidae*), up to species such as the

Capercaillie (*Tetrao urogallus*), where males can be over twice the weight of females (Cramp and Simmons 1980; Bennett and Owens 2002). Furthermore, it is not necessarily always the male which is the larger sex, for example, in the European sparrowhawk (*Accipiter nisus*), the males weigh 150 g but the females are 60% heavier at 260 g (Newton 1986). There have been several attempts to explain sexual size dimorphism in birds (e.g. Payne 1984; Jehl and Murray 1986; Mueller 1990) but opinions differ as to whether the variation is best explained by sexual selection, or by other factors (Andersson 1994).

Darwin (1871) suggested two routes through which size dimorphism could occur. First, for animal groups such as fish and insects, larger females produce more eggs, so have a reproductive advantage. Second, in mammals, males that are larger are more likely to win intra-sexual competitions to access females. For birds, it is possible that either of these routes could lead to sexual size dimorphism but ecological factors could also be important. For example, size dimorphism could reduce competition between the sexes through niche separation, which could evolve through differences in parental care roles, or through differences in the age at maturity (Andersson 1994). There could even be sexual selection favoring small males if mate choice is based on flight displays, because small males tend to be more maneuverable in flight (Andersson and Norberg 1981).

As discussed above, however, it is necessary for the sexes to be under different selection pressures for dimorphism to evolve. In most, but not all, birds which exhibit sexual size dimorphism, it is the male which is the larger sex. This could occur, for example, if males gain a mating advantage from being larger than average in comparison to other males, yet larger size carries some cost, such as a physiological cost of maintenance. Females would suffer the cost but without the sexual selection advantage, so would remain small, or even reduce in size over time, whereas males would increase in size until the sexual selection benefits of being large were matched by the natural selection costs. Such a process could result in the evolution of size dimorphism (Andersson 1994). A nice example comes from work on Darwin's ground finch (*Geospiza fortis*) where the various partly opposing selection forces have been identified, in relation to body size, for each sex (Price 1984). Females are under selection to be relatively small, because small females survive better when they are young and can start breeding earlier, although as they become older, selection favors larger females, so the pressures change with age. For males, there is also a survival advantage for young males to be small but, as with females, this is reversed as they get older, when being larger is an advantage. Males have an additional sexual selection pressure, however, that favors large males because they have a higher reproductive success. Overall, the net balance of the selection pressures is for males to be larger than females (Price 1984).

In a comparative analysis which tried to explain some of the patterns in sexual dimorphism across bird species, Ian Owens and I found that size dimorphism was under selection pressures different from those affecting plumage dimorphism (Owens and Hartley 1998). While color dimorphism

was related to inter-sexual selection through mate choice for extra-pair matings, size dimorphism was not. Instead, size dimorphism was associated with the social mating system, so that larger size differences between the sexes were found in species where polygyny was most regular (Table 4.1). We also found that the degree of size dimorphism was positively associated with sex bias in nestling provisioning behavior and active brood defense; the sex with multiple mates often reduces parental care to the brood in polygynous species. These findings support the conclusions of previous studies such as an analysis of New World blackbirds (Icterinae), which showed that size dimorphism was associated with intra-sexual competition (Webster 1992). Intra-sexual selection favors males that are larger than average, as they are more likely to win contests over access to females, or to defend better or larger territories which support more breeding females.

Further evidence that intra-sexual selection is important in the evolution of sexual size dimorphism comes from those species where the female is larger than the male; so-called reversed size dimorphism. Reversed size dimorphism is found commonly in four avian taxa: the Accipitridae (hawks, buzzards and eagles), Falconidae (falcons), Strigiformes (owls) and Charadriiformes (waders), and much effort has gone into trying to explain the patterns of dimorphism in these groups. In the Charadriiformes the pattern of sexual size dimorphism is variable; either the male or female can be the larger sex, or there can be very little difference between the sexes. In a comparative analysis that controlled for the potentially confounding variable of shared phylogeny, Székely *et al.* (2000) showed that sexual size dimorphism in the Charadriiformes was strongly associated with the social mating system. Males tended to be larger in polygynous species and females tended to be larger in polyandrous species. Furthermore, they ruled out any effects that might have been due to natural selection for niche separation between the sexes. Selection via niche separation should lead to a divergence between the sexes in bill morphology especially in those species which feed in the same territories or home ranges, such as those exhibiting biparental care. However, species with biparental care were not more likely to have sexually dimorphic bills compared to species with uniparental care. There was also a link between flight displays and reversed size dimorphism in the Charadriiformes; males tended to be smaller in those taxa where acrobatic flights are used in sexual displays (Jehl and Murray 1986; Krüger 2005). Small males are able to produce acrobatic aerial displays more cost effectively than large males because of the aerodynamic energy savings. There are, however, quite a few exceptions to this general pattern and, if we look beyond the Charadriiformes to the larks (Alaudidae) and pipits (*Anthus* species), we can find many species where the males are the larger sex despite being reliant on flight for their song displays (reviewed in Andersson 1994).

In the birds of prey (Accipitridae, Falconidae and Strigiformes) there are several hypotheses which could account for their reversed sexual size dimorphism but these have been nicely summarized under three main

categories by Krüger (2005). The ecological hypothesis predicts a divergence in sizes in response to competition between the sexes; the role-differentiation hypothesis predicts that females should be larger, either as a result of selection for the formation of larger eggs (females get bigger) or increased male agility as a hunter (males get smaller); and the behavioral hypothesis predicts an increase in female size as a result of selection pressure for females to dominate males or compete for them, or for males to become smaller to be more agile in display flights (Krüger 2005). A comparative analysis across the different species of birds of prey supports the link between hunting strategies and reversed sexual size dimorphism. Across the three predatory bird taxa, the explanation with most support was the ecological hypothesis, specifically that males had become smaller under natural selection pressure to be more efficient foragers as they provide much of the food during periods of incubation and early chick rearing (Krüger 2005). A study of the Tawny owl (*Strix aluco*) similarly demonstrated that being small was an advantage for males because, as the main providers of food to the nestlings, they were under greater selection to be more aerodynamically efficient (Sunde *et al.* 2003). Both these conclusions are in agreement with one of the findings of our study across a wider range of bird taxa, which showed an association between sex bias in nestling provisioning and the extent of size dimorphism (Owens and Hartley 1998). The reason why female birds of prey are usually the larger sex, and have not reduced body size in a similar way to males, remains open to question to some extent. It is most likely due to some opposing selection pressure to be large, possibly because large females can lay more or larger eggs or can, in some other way, have a higher reproductive rate. So, it is clear that although reversed sexual size dimorphism is common in predatory birds, as it is in the Charadriiformes, it has evolved under different selection pressures.

4.4.1 Sexual Dimorphism and Body Size

In general, there is a positive correlation between body size and the magnitude of sexual dimorphism (ratio of male to female body size); sexual size dimorphism is more extreme in larger species. The pattern seems to hold for a wide range of taxa including some birds (Abouheif and Fairbairn 1997; Fairbairn 1997; Colwell 2000; Fairbairn 2005) and is called Rensch's rule, after the scientist who first identified the pattern (Rensch 1950). There are however, exceptions to the rule, for example the pattern is reversed in some animal groups such as lizards (Stamps 1983) and weasels (Ralls and Harvey 1985), and absent in others, such as seals (Lindenfors *et al.* 2002) and some bird groups (Tubaro and Bertelli 2003). The mechanisms underlying Rensch's rule are still a matter for some debate but potential explanations are reviewed by Andersson (1994). First, theoretical models suggest that genetic correlations for body size between the sexes result in simultaneous body size evolution, even when the selection pressures act on only one sex (Maynard Smith 1978; Lande 1980; Lande and Arnold 1983; Lande 1987). So, if selection favors large males, the genetic correlation between the sexes will drag female body size up

as well. Other hypotheses suggest that natural selection is less restricting on expressions of sexually selected traits, including body size, in larger species because they are less prone to predation, they are likely to have fewer other species to compete with, and they are energetically more efficient; fighting efficiency, especially with weapons such as spurs, becomes more effective with increased body size; there is strong selection for small female size in large species; or finally, there is strong selection for large female size in small species (Andersson 1994).

An analysis of the Charadriiformes sheds some light on the problem and suggests that for shorebirds at least, the pattern is best explained by sexual selection (Székely *et al.* 2004). In the analysis, Székely and his colleagues showed that the Charadriiformes exhibited the full range of Rensch's rule; in species where the male is larger than the female, sexual size dimorphism increased with body size, and in species where the female is the larger sex, size dimorphism decreased with increasing body size. The pattern was best explained by the effects of, and interaction between, sexual selection on males to be small, for agility during aerial sexual displays, and large, for success in male-male competitions. They also excluded some ecological explanations of the pattern; neither habitat productivity nor feeding ecology explained Rensch's rule in the shorebirds. In hummingbirds (Trochilidae) Rensch's rule is also exhibited in full but here the pattern is explained by a combination of stabilizing selection on females and both natural and sexual selection effects on males (Colwell 2000). Overall, the differences in selection pressures acting upon the sexes once again lead to sexual dimorphism but are further complicated by the outcomes being body size dependent. While males are more prone to evolve as a result of sexual selection, females might be dragged along due to genetic correlations but may be limited in how far they can be dragged (Figs. 4.2 and 4.3). At the small end of the body size spectrum, females may be selected to be relatively large because that increases fecundity, survival or competitive ability (e.g. Reynolds 1972; Snyder and Wiley 1976; Wheeler and Greenwood 1983; Brown and Brown 1998; Forero *et al.* 2001; McDonald *et al.* 2005), whereas at the large end of the size spectrum they may be selected to be smaller because smaller individuals can mature faster and potentially breed earlier (Stearns 1992).

4.5 CONCLUSIONS

Ultimately, sex differences are the net result of multiple selection processes that may be complimentary or opposing. and although we can identify many of the key factors which are involved it is unlikely that there is a single explanation for the evolution of sexual size or color dimorphisms. The many comparative analyses which explore the evolutionary patterns across species provide useful pointers to inform about the likely selection pressures involved in the evolution of dimorphism. There is, however, the limitation that they are correlational studies and do not lend themselves to experimentation. It would be useful to see more experimental field studies on species where the selection

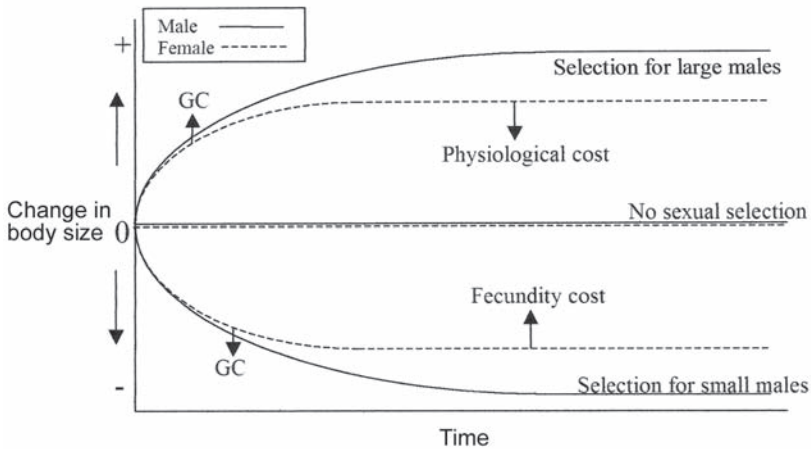


Fig. 4.2 Schematic illustration of how body sizes might change due to sexual selection on males to be either larger (male-male competition) or smaller (sexual selection for aerial displays), when there is a genetic correlation (GC) between female and male body size. In the absence of sexual selection, body sizes of both sexes are at their optima in relation to natural selection, although they may still differ. When females are dragged higher than their optimal body size they suffer physiological costs of large body maintenance. When they are dragged below their optimal body size they suffer fecundity costs. Original.

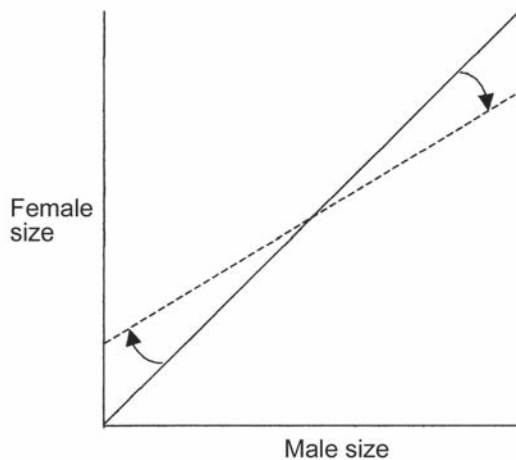


Fig. 4.3 The relationship between body sizes of males and females should be distorted away from the 1:1 slope (solid line), as indicated by the arrows, when males are under greater sexual selection than females (dashed line) (see Figure 4.2). This leads to the pattern described in Rensch's rule, where sexual size dimorphism decreases with body size in species where the female is the larger sex but increases with body size in species where the male is the larger sex. Original.

pressures which lead to size dimorphism are partitioned and quantified. Such experimental studies are quite widespread in the study of plumage color and ornaments (e.g. Zuk *et al.* 1992; Gustafsson *et al.* 1995; Griffith *et al.* 1999; Jones and Hunter 1999), perhaps because plumage traits are easier to manipulate than body size. More detailed studies which quantify the components of selection in relation to dimorphism would also be useful.

4.6 ACKNOWLEDGMENTS

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Sexual Selection, Signal Selection and the Handicap Principle

Amotz Zahavi

5.1 INTRODUCTION

Darwin (1871) suggested the mechanism of sexual selection to explain the inheritance of traits that are limited to one sex, “Sexual selection depends on the success of certain individuals over others of the same sex in relation to the propagation of the species.” He emphasized, repeatedly and vividly the extravagance and the burden that evolves in males as a consequence of female choice, suggesting that such traits “must be in some manner highly important; and we know that they have been acquired in some instances at the cost not only of inconvenience, but of exposure to actual danger” (p. 399). He wondered: “...it is doubtful how the more attractive males succeed in leaving a larger number of offspring to inherit their superiority in ornaments or other charms than the less attractive males; but I have shewn that this would probably follow from the females — especially the more vigorous females which would be the first to breed, preferring not only the more attractive but at the same time the more vigorous and victorious males” (p. 400).

Darwin emphasized repeatedly that sexual selection could function only if the most attractive males were also the most vigorous ones. He did not ask why females should be attracted to wasteful extravagant males, and did not ask how the waste could be correlated to vigor, probably because common observations showed that these males were, in fact, the most vigorous ones.

In 1975 I answered these questions by introducing the handicap principle (Zahavi 1975). The handicap principle considers the burden imposed by extravagance as a handicap that tests the quality of the signaler. Signalers of a higher quality can develop the handicap more than signalers of a lower quality. Hence, a female selecting a male with a bigger burden is getting a male

of a higher quality. The handicap principle is the mechanism that explains how the more attractive males must be of a higher quality than the less attractive ones. In 1977 I suggested that the handicap principle is effective not only in mate choice, but in the selection of all signals, that is, that every signal, sexual or other, should contain handicaps to enable the receiver to ascertain its reliability (Zahavi 1977a).

In his definition of sexual-selection, Darwin mixed traits that are signals, such as extravagance, with efficient traits, such as size and weaponry. This may be the reason why he found it difficult to define a clear differentiation between natural selection and sexual selection: "...in most cases it is scarcely possible to distinguish between the effects of natural and sexual selection" (p. 257); this may also be the reason he was not successful in convincing the scientific community that sexual selection operates in a different way than other selection mechanisms (Mayr 1972; see however Mayr 2001). Nonetheless, sexual selection as defined by Darwin was, and still is, widely used today to refer to the selection of traits involved in sex, possibly because of the major selective force of reproduction.

In 1981 (Zahavi 1981a) I pointed out that the selection for signals operates by a different selection mechanism than the selection of all other traits. I suggested that two distinct selection mechanisms operate within natural selection: utilitarian selection, which is selecting for efficiency, by which all traits that are not signals are selected; and signal selection, the selection of signals, which requires investment that often results in considerable waste (handicaps) to ensure the reliability of signals. This suggestion supports Darwin's intuition that there are two different selection mechanisms that operate in nature. But the differentiation between them is not the same as that proposed by Darwin.

5.2 FISHER'S MODEL

5.2.1 Introduction

Before discussing the handicap principle and its broad implications, I would like to discuss Fisher's model of mate choice (1958), which is still widely used. Fisher assumed that by being wasteful, extravagant males were less adapted than unadorned ones. Since he believed that, like any other adaptation, female's preference must have evolved by natural selection, he asked why would females be attracted to extravagant and wasteful traits. In his model, he tried to explain how such a preference could have evolved and be maintained.

According to Fisher's model, a signal of mate choice like the long tail of the Peacock (*Pavo cristatus*) could have evolved in the following manner: a mutant peahen started selecting a mate according to the length of its tail, preferring a longer tail, rather than mating at random. Obviously, heavier and bigger males had longer tails than smaller males did, since a heavier body requires a longer tail to steer it. A female that picked a male by the length of its tail mated with a heavier male, which could be an advantage to her progeny.

Consequently, such a preference could spread in the population. Fisher termed this initial evolutionary sequence the “preference stage.” Once many females acquired the preference, males could benefit from increasing the length of their tail more than was required for efficient movement. The burden of the extra length was compensated for by the preference of the females. The more females preferred males with longer tails, the more the males benefited from increasing the length of their tail.

The evolutionary response of males to the female’s preference started what Fisher termed a “runaway process”, resulting in males growing their tail as long as they could. Fisher’s model assumes that once all males invested in growing their tails, tail length was no longer correlated to quality.

Fisher’s model justified the continued preference of the females for a long tail by the fact that all or most females prefer it. Fisher pointed out that a female that would depart from the convention and mate with a male with a short and efficient tail would produce male offspring that would not find a mate among the daughters of the females that still prefer long tails, since these daughters inherit from their mother the preference for long tails. Later on, mathematical models demonstrated that any random preference by females may lead, through a runaway process, to extravagant traits, without any correlation to quality (Lande 1981).

5.2.2 What is Wrong with Fisher’s Model

First. Fisher assumed that the correlation between tail length and quality was lost during the “runaway process”. It is obvious, however, that a male of a higher quality can carry a heavier burden than a male of a lower quality. I would like to suggest that, contrary to Fisher’s assumption, elongated tails do reveal differences in male quality — in fact, they do so better than short and efficient tails can (Petrie *et al.* 1991).

Second. Fisher’s model depends entirely on the assumption that a mutant female that stops paying attention to tail length will have sons with short tails. These sons would be unable to mate, because the majority of females prefer males with elaborate tails, and dissident lines will eventually disappear. However, if the mutation occurs at the stage at which, according to Fisher, all males possess long tails, then the sons of the dissident female will inherit the long tails of their fathers, and thus find mates.

Third. Still, the males differ in qualities other than tail length, and they advertise these qualities by other modalities. Birds, and probably all animals, select mates by more than a single marker of quality: birds advertise for potential mates by singing, by colorful displays, by movements, and by growing tails, crests etc. If one of these markers ceases to correlate with quality, a female that stops taking that marker into consideration and relies instead on the other existing markers would make a better choice than females that continue to take into account the useless marker. If, as Fisher claims, long tails are not correlated to quality, the mutant female’s preferences are now better

than the preferences of all other females, the number of her daughters would increase in the population, and the number of females preferring long tails would decline. Once females stop preferring long tails, a male that would grow a short and efficient tail would be more successful than males with long tails, and long tails would disappear by a process similar to that suggested by Fisher's model (the runaway process), but in the opposite direction.

Fourth. Fisher's model cannot explain the fact that signals of mate choice often also deter rival males (see Berglund *et al.*, 1996). Fisher was aware of that (Fisher, 1958, 2nd edition, p. 155/6), but could not explain it. He therefore suggested that evolution would "eventually" eliminate the rivals' unwarranted reaction to what he called "war paint". The handicap principle, on the other hand, can explain the evolution of extravagance in signals that deter same-sex rivals just as well as in signals used to influence mate choice.

To sum up. Before males invested in increasing their tail length, the tail was an efficient instrument. It was correlated to body size, and large individuals had longer tails because they needed them. At that time, although females benefited from paying attention to tail length, the tail was *not* a signal. Once males started to increase their tail length as a signal, the tail was no longer as efficient as before, handicapping its bearer (Fig. 5.1A). Each male could invest in increasing its tail length according to its own phenotypic quality. The increased length made it easier for females to perceive differences in male quality, and males with extra long tails benefited by being chosen by females. Males that increased their tail size beyond the measure that their phenotypic quality would allow were weeded out by natural selection — that is, they paid a cost (a reduction in their fitness.) Evolutionary biology defines "cost" as a loss in fitness. But honest signalers gain fitness by signaling. Only cheaters lose — that is, they pay the cost of their handicaps. Hence, I now prefer to use the term "investment" rather than "cost" for the extra burden of the handicap.

Ryan (1990) suggested that some signals evolve because receivers are already attentive to them and signalers can "exploit" that pre-existing attention. I suggest that a preference by the receiver always precedes the evolution of signals (Zahavi and Zahavi 1997). However, a preference can prevail only for reliable signals that reveal quality, not because the receiver is "pre-adapted" to it, or because the signal is preferred by "everybody" for no good reason, as suggested by Fisher's and similar models.

The handicap principle suggests a mechanism by which a signaler can ensure the reliability of the message encoded in a signal: the signal itself handicaps the signaler in something that is related to the information provided by the signal. The investment in such handicaps should be differential: it should be affordable for an honest signaler but not to a cheater. Thus, although the handicap principle was formulated to explain the evolution of extravagant signals of mate choice, it can just as well ensure the reliability of other signaling systems, in reproduction as well as all other signals, like threat signals, begging calls etc. (Zahavi 1977; Zahavi and Zahavi 1997).

5.3 OBJECTIONS TO THE SUGGESTION THAT ALL SIGNALS INVOLVE HANDICAPS

For many years the handicap principle was rejected because mathematical models claimed to prove that it was wrong. In 1990, however, Allen Grafen vindicated the handicap principle mathematically, showing that it may work even in mathematical models (Grafen 1990a,b).

Grafen (1990) and Maynard Smith (1991) assume that when there is no conflict between signaler and receiver, there is no need to invest in the reliability of signals. But in actual life there is a potential for conflict even between the most cooperative of parties, such as parents and offspring (Trivers 1974). I suggest that this potential for conflict shapes the pattern of signals: the common interest only requires that a signal be something that a receiver would respond to but a conflict of interests demands that signals be reliable. According to the handicap principle, reliability is achieved when the pattern of the signal restricts the ability of a cheater to benefit from using it to deliver an incorrect message. Handicaps can even be useful in preventing mistakes in signaling systems within the multicellular body; for example the harmful chemicals used in nerve communications (Zahavi 1993; Zahavi and Zahavi 1997).

Maynard Smith and Harper (2003) suggest that there are two alternative explanations for the reliability of signaling systems: the handicap principle, and 'indices of quality'. They define an 'index' as a signal whose form and intensity are physically associated with some quality of interest to the receiver: "...in effect, it is an unfakable signal that is reliable because it cannot be faked".

I suggest that all signals are 'indices'. They advertise or amplify some qualities in the signalers that are of interest to the receiver of the signal. The attention of the receiver to certain traits in the signaler may induce the signaler to exaggerate these traits in order to help the receiver to assess small differences between apparently similar signalers, or between different situations of the signaler. Any exaggeration, however slight, means that the trait is no longer at the optimum attained by natural selection, and thus involves an additional investment. The magnitude of the investment is proportional to the possible gain by cheating. If the additional information gained by signaling is small, or of little importance, the investment in the signal can be quite low. The investment is always differential — that is, it is easier for the honest signaler than for a cheater, and its scale is constantly being adjusted by natural selection.

5.4 HANDICAPS, COSTLY SIGNALING, AND HONEST SIGNALING

5.4.1 Introduction

Before I suggested the handicap principle, researchers did not consider signals to be necessarily honest, and often suggested that signalers try to

deceive the receivers. Since 1975, when the handicap principle was first proposed, a large number of studies have demonstrated that many signals are in fact honest — that is, correlations were found between the dimensions of the signals and some quality of the signaler (Andersson 1994). Many terms have been suggested for such signals: “honest signaling”, “reliable signaling”, “costly signaling” and so on. In most cases, however, the authors did not ask what it is that makes the signals honest — that is, what are the handicaps that prevent cheaters from using the signals. It is often not easy to find out what the handicap or the message is in a certain signal, especially in small lines or color patches. But finding it can be highly rewarding.

The concept of set-specific signals assumes that such signals have evolved in order to mark an individual as belonging to a certain species, or to a certain gender or age group within the species. It is assumed that they are the consequence of the common interests of members of a set to set them apart from other sets. Since such signals benefit all parties, the argument goes, they are not involved with conflicting interests, and therefore there is no room for cheating and no need for handicaps. I suggested, on the other hand, that these signals also evolve out of competitions among signalers for the attention of the receiver. It is easier for a receiver to compare contestants along certain standards. It is thus the receiver that demands that signals should be performed in standard ways. The standards of competition help show differences that otherwise would not be clearly apparent. In other words, I suggest that the standard pattern of a particular display evolved in order to demonstrate clearly the differences between otherwise apparently similar signalers or between different circumstances. I therefore suggest that set-specific signals are in fact the standards for comparison between members of the set, rather than markers tagging the individual as a member of that set. The pattern of the markings and their placement on the body of the signaler enable us to infer the message encoded in the signal.

5.4.2 Can One Use the Reaction of a Receiver to Decode the Information Conveyed in a Signal?

People often interpret the message encoded in a signal according to the reaction of receivers. A signal that results in a retreat of an opponent is considered a threat display. A signal that attracts a mate is considered a display of the signaler’s quality or its interest in a mate. However, the same signal that attracts a mate often deters a rival. This is common in signals used by males in the breeding season. Instead of suggesting that such signals carry two distinct messages, I suggest that it is simpler to see the message — the information provided by the signal — as being the same; each receiver reacts to that same message according to its own interests. A signal that displays in a reliable way the strength of a male does not say either “stay away” or “come to me,” but rather “I am strong.” This same message attracts a mate and deters a rival. The specific content of the message may be deduced from the handicap imposed by the signal. For example, the burden of the long and heavy tail of

the peacock displays in a reliable way the strength of the male. Stronger males can carry heavier tails than weaker males and can rattle them more quickly. This explains why a rival is deterred by such a display and why a female is attracted. The message to the rival and the mate is the same — the strength of the signaler.

5.4.3 The Connection between the Signal and its Message

Once we understand that the pattern of a signal handicaps the signaler in something that is related to the information provided by the signal, we have a connection between the pattern of the signal and its message. This logical relationship enables an observer to deduce the particular quality displayed by a particular signal, whatever the modality of the display, as the following examples show.

Elongated tail feathers handicap flight and can therefore honestly advertise the ability to fly. This was shown by Møller (1994) for the barn swallow (*Hirundo rustica*). But such feathers cannot serve to display how many hours a day a male needs to invest in feeding, for example. On the other hand, a male can display the amount of free time at its disposal by investing time in singing, assuming that it cannot both sing and feed at the same time (Wilhelm *et al.* 1982).

The White pelican (*Pelecanus onocrotalus*) grows during mating season a bump on its forehead. This bump restricts its vision and may interfere with its fishing. A pelican that can grow such a bump displays its ability to fish in spite of that interference. Growing such a bump elsewhere on its body would not have displayed that same information. A young pelican, or an adult unable to find abundant fish, will not be able to survive with such a handicap; only adults who are in position to breed grow the bump.

Small color markings on plumage function in signaling. The size of such markings often display meaningful variation. For example, the adult Great gray shrike (*Lanius excubitor*) develops bold eye stripes. One can figure out the direction of the shrike's gaze by observing the apparent changes in symmetry of the eye lines. It is therefore reasonable to assume that the lines help the shrike display its interest in a mate or a rival more clearly and over longer distances. A shrike that is sure of its position in the territory may gaze at an opponent continuously, without shifting its gaze to check whether it is endangered from behind. For an adult, it is a reasonable investment since it benefits from threatening and has the potential to win even if surprised from behind. It is a handicap because the bold lines through the eyes would expose the insecurity of less dominant adults, or of the same individual under different conditions. A young shrike cannot afford that investment, it has to look around. This may be the reason why young shrikes have fuzzy gray eye lines. With this interpretation, one can see the function of the line as a handicap and the signal as benefiting the individual, unlike the common interpretation that the differences in the lines specify the set of adult shrikes as distinct from young shrikes for the benefit of all.



Fig. 5.1 **A.** Peacock (*Pavo cristatus*). Once males started to increase their tail length as a signal, the tail was no longer as efficient as before, handicapping its bearer. Each male could invest in increasing its tail length according to its own phenotypic quality. Males with extra long tails benefited by being chosen by females but if they increased their tail size beyond the measure that their phenotypic quality would allow were less fit and were weeded out by natural selection.

B. Arabian babblers (*Turdoides squamiceps*) in a “water dance”. These desert birds do not miss the opportunity to bathe, either in the rare occasions of rain — or when water is presented. Following thorough wetting they clump, each bird preening itself only, as they do in the morning dance. This is different from sessions of allopreening that happen throughout the day. **Inset.** Allofeeding during the replacement of a sentinel. **C.** Babblers in a “morning dance” on a branch. Photos A. © Barrie Jamieson. B, C. © Amotz Zahavi.

A color mark may also impose a cost merely by providing more precise information on the quality of the signaler. Such markings were classified by Hasson (1991) as amplifiers. For example, many elongated fishes have lines along their bodies. The line itself may be very cheap to produce. However, such lines clearly display differences in body length among individuals that otherwise would have seemed to be of equal length. What kind of a handicap can be involved in providing more precise information about the true length? — The longest individual in a given group clearly benefits from showing its precise length, either when contesting with other individuals over food or territory or when being chosen as a mate. The individual next to it in length loses in a sense, because the line shows clearly that it is shorter — a fact that may not have been as clear without the line. Still, the second in length is longer than the rest of the group except the first. It therefore gains when competing with them, and so forth. However, even the longest individual may sometimes lose, when an individual even longer than itself moves to the neighborhood. Providing honest information about quality always involves the risk of a loss. Like all handicaps, the risk is differential: it is greater for the shorter individuals than for the longer ones.

Why, then, do inferior individuals display their quality by a standard that reveals them to be inferior? They do so because all inferiors are not equal. In any competition among them, the receivers of the signal require the same standards, as they wish to know which of them is least inferior so as to choose the better among them. The receiver may overlook an individual that cannot be compared to other contestants. Thus, even signals that are usually considered as merely set specific are loaded with the handicap of displaying the truth more precisely.

5.4.4 The Handicap in Carotenoid Signals. Or: Can a Signal be Both Honest and Beneficial?

Carotenoid signals may illustrate the difficulty in finding the cost of a signal to cheaters. Hill (1990; Chapter 2) established the fact that carotenoid coloration is correlated to the phenotypic qualities of the House finch (*Carpodacus mexicanus*). At first he suggested that the handicap is in the ability of the signaler to collect carotenoids. However, the variation in coloration persisted even when birds had free access to carotenoids. It was therefore later thought that a tradeoff between the use of carotenoids by the immune system may limit sick birds from developing carotenoid coloration. However, McGraw *et al.* (2005) found that even a small deprivation of food (while supplying ample carotenoids in the unlimited drinking water) limits the use of carotenoids. McGraw (2005) concluded that: “animals reap benefits from components of their sexual displays”. “Carotenoid-based colors have served as ideal models for studying the honesty-reinforcing mechanism underlying sexually selected traits, because the very pigments used to become colorful also have antioxidant and immunoregulatory properties that allow individuals to signal their superior health to prospective mates...”. However,

carotenoids, depending on their concentrations, are not only antioxidants, they often are lipid pro-oxidants (Haila 1999). This may be the reason why birds under even mild dietary stress cannot carry high carotenoid concentrations in their blood. The colorful males may be signaling their superior health by the fact that they can overcome the handicap of the pro-oxidant effects of the carotenoids (Zahavi and Zahavi 1997).

5.4.5 The Interaction between Color, Movements and Images in Displays

Sometimes researchers investigate variations in color patches without paying attention to the way the color enhances the variation in the displays of body structures. Darwin suggested that movement displays evolved to demonstrate and enhance the effects of certain body markings and decorations. I agree that displays of color and movement interact in their effects, though I suggest that as a rule color helps in displaying a motion or a structure rather than the reverse.

It is now well established that symmetry is correlated to quality (Thornhill 1992). Wing patches may amplify symmetry (Jablonski and Matyjasiak 2002). The wing patches are not the message. The message is in exposing the degree of symmetry of the wings. The interest of the receiver in the symmetry of the wings as a correlation to overall quality may have started a process that pushed for evolution of the most symmetrical pair of wings, just like the one that caused the extension of the peacock's tail. I do not know the quality and quantity of the investment required by an organism to develop a perfect symmetry. I suggest, however, that it requires an investment that low quality individuals (whatever that quality is) are unable to afford, while a higher quality individual can invest in order to display symmetry, even though a perfect symmetry may not be essential for efficiency.

Many birds erect their crown feathers during interactions with other birds. This erection is often accentuated by simple or elaborate crests as is the case of the Hoopoe (*Upupa epops*). The crest displays the variation in that posture more clearly. The handicap in erecting the crown feathers may be in lowering the efficiency of the signaler to observe or to move as efficiently as it can. A bird attentive to nearby danger and ready to move has sleek crown feathers. Madden *et al.* (2004) have shown that in the Spotted bowerbird (*Chlamydera maculate*) bower owners had larger crests than non-owners and females, and that crest area provided the most accurate predictor of a bird's sex and status. The crests are made conspicuous during display to both males and females. During such displays the males turn their head and nape towards the females, exposing the crest. The males of two closely related species (*C. cerviniventris* and *C. lauterbachii*) also turn their heads and napes towards the females, although these species do not possess crests. The authors suggest that these species lost their ancestral crests, but not the movements by which the crests were made conspicuous. It may be, though, that the crest evolved in the Spotted bowerbird in order to amplify the movements.

5.4.6 The Cost in Vocal Signals

Vocal threat signals are often given to far away rivals by rhythmic shouts. The more evenly the notes are separated from one another, the bigger the threat. Spacing of vocalizations may be considered as a trivial investment. However, it demands concentration by the signaler. Hence a rhythmical threat displays the fact that the signaler can and is motivated to concentrate on threatening, without having to look around to collect more information to decide whether to attack or withdraw.

5.4.7 Conclusion

Maynard Smith and Harper (2003) attempted to divide reliable signals into signals that are handicaps and others that are indices that are not involved with handicaps. I suggest that all signals, both large, prominent ones like the peacock's tail and small ones like color lines or patches, are honest and reliable indices of certain qualities (including motivation) that are rendered reliable by the investment (handicap) involved in them, even though it is not always obvious what handicaps they impose. Cheaters, that without the signals could have benefited from being considered as of a higher quality than they really are, pay a cost for revealing their real quality.

5.5 HANDICAPS IN SOCIAL BEHAVIORS

5.5.1 Clumping, Dancing and Allopreening

Babblers (*Turdoides squamiceps*) clump frequently, like many other social birds living in permanent groups or pairs. They do so either while resting, or during social activities such as allopreening (Dattner 2005) play (Pozis-Francois *et al.* 2004) or during the morning dance (Ostreicher 1995) (Fig. 5.1B,C). Most other birds tend to keep their individual distance to enable them to fly and move freely without physical interference from neighbors. Clumping is thus a burden, but babblers seem eager to do it. The investment in clumping can be interpreted as a test of friendship. A babbler that clumps with another individual displays its readiness to take on a burden in order to bond with that individual. Accepting the invitation to clump demonstrates the interest of other individuals in the inviting one. Additional social information is transmitted during allopreening and clumping (Zahavi 1978; Zahavi and Zahavi 1997; Dattner 2005).

5.5.2 The Importance of Social Prestige

Babblers use very little aggression among group members. For group living birds threat is more costly than for solitary ones. A bird that threatens but does not substantiate its threat if the threat does not cause its desired effect may lose social prestige, that is, lose the potential to threaten other group members who witnessed its failure. I suggest that for this reason altruistic acts often replace aggression in cooperatively living animals. A babbler that can act as a

sentinel while others are feeding, or risk its life to defend other babblers, provide food to other individuals and tend to young that are not its own gains social prestige and may dominate without the use of aggression. Like a peacock's tail, social prestige is an indicator of quality. It can attract collaborators (mates and helpers) and deter rivals. Babblers invest daily in their altruistic displays because social prestige, unlike social rank, is a parameter that may change from one day to the next because of events within the group or interactions with neighboring groups or with predators (Zahavi and Zahavi 1997).

It is easy to observe and describe dominance, but studies of social behavior have largely ignored the subtler parameter of social prestige (or social status). It is not easy to measure social prestige. However, it is a mistake to ignore it. I believe that social prestige is an ever-present parameter that may explain several other hitherto unexplained phenomena.

5.5.3 The Evolution of Altruism

One of the most important contributions of the handicap principle is in explaining the adaptive significance of what were considered to be altruistic acts, interpreting them as signals for the claim of social prestige. Altruism has been defined as 'an activity that benefits another but is harmful to the altruist'. Babblers, like many other cooperatively living birds, display many altruistic adaptations. They help to tend to offspring that are not their own, they feed other adults (Kalishov *et al.* 2005), they act as sentinels when other members of their group feed, they mob predators and defend the common territory against other babblers rather than letting others fight for it. Complex theories, such as group selection, kin selection, and reciprocity have been suggested in order to explain how these activities can provide indirect advantage to the altruists. We have found that babblers compete with one another to perform the altruistic activities, and they often also interfere with the altruistic activities of others. These observations suggested that the altruist gains directly from its altruistic activity (Zahavi 1977; Carlisle and Zahavi 1986; Zahavi and Zahavi 1997; Kalishov *et al.* 2005).

The altruistic act can be considered to be an investment (handicap) in the claim for social prestige, demonstrating the reliability of the claim. It is obvious that the idea that the altruistic act provides a direct advantage to the altruist, render the above-mentioned theories of indirect benefits superfluous.

5.5.4 A Cooperation of Two and the Advantage of Adopting a Social Parasite

Although a male and a female are essential for sexual reproduction, they are not always essential for rearing the young. Trivers (1971) pointed out that an individual that could exploit another and does not do so is an altruist. Why should a parent feed at the nest rather than leaving the job to its mate, as some species do? Most studies of the conflict between the sexes deal with situations that justify such exploitations. However, many more species do not exploit

their mates and often individuals invest in their offspring although their mates are ready to provide the offspring with the same benefits. I suggest that in addition to their direct contribution to the individual's reproduction, the efforts of a parent to invest in incubation and in tending to the young may be signals of quality and as a demonstration of the signaler's interest in the collaborative effort. In this they are similar to their role among helpers in cooperative breeding species. This may also explain the common phenomena of breeding out of season, when it is obvious that the breeding attempt would fail. The investment in the collaboration is a reliable signal for the motivation of the individual to collaborate and in its ability to invest in the next year's collaboration.

Even tending to the nestling of other species can serve a similar purpose (Zahavi and Zahavi 1997). By tending to the social parasite in their nest, a pair that has lost the chances to raise its own offspring in a particular breeding season can demonstrate to each other and to their neighbors that they are still capable parents. This may explain why a small song bird tends to a huge, easily recognizable cuckoo nestling over several weeks (see Chapter 10), a highly maladaptive trait that could have easily been selected out by utilitarian natural selection. The Hooded crow (*Corvus corone*) often raises its own offspring together with those of the Great spotted cuckoo (*Clamator glandarius*). The cuckoo nestlings and fledglings beg much more loudly than the crow's own nestlings and follow their foster parents with aggressive and very loud vocalizations; the parents feed both their own nestlings and the cuckoo. Feeding their own crow nestlings is of course a direct advantage to the parents, while feeding the cuckoo provides them only with the prestige of raising it. Hence, in order to increase that prestige, the cuckoo advertises the feeding event by loud vocalization, in spite of the risk of predation. This suggestion has not yet been considered in studies of social parasitism.

5.6 SIGNAL SELECTION AND UTILITARIAN SELECTION

In 1981 I suggested that natural selection involves two modes of selection: utilitarian selection, that tends to increase the efficiency of traits, and signal selection, that reduces the efficiency of certain traits for the sake of reliability. The evolution of all traits, including signals, is restricted by the need to evolve other essential traits. The differences between the above two modes of selection can best be understood by predictions of the outcome of these two modes of evolution when conditions change, easing these restrictions: when the investment required for the development of a particular utilitarian trait is reduced, the use of that trait may increase, or it may not change. It is not dependent on the fact that other individuals can use it equally well. This is not the case with signals. In order to be reliable, signals require differential investments. If the investment in the reliability of a signal is lowered to the extent that all individuals can perform it alike — the signal can no longer provide reliable information on differences between signalers and will go out

of use. I suggested that this process is analogous to the inflation of money in human economics: money loses its value when all people can have as much money as they wish. In the first stage its use increases tremendously (inflation), but soon it becomes obsolete and the currency is changed.

It would be very difficult to test the above proposition because evolutionary processes evolve over long periods of time. I speculated (Zahavi and Zahavi 1997) that inflation in the use of signals may be responsible for the elimination of color displays in island-drakes. Lack (1970) attributed the loss of color in mallards and other island-ducks to the fact that having no other duck species on the island, drakes had no more use for their species specific coloration, and consequently lost them. An alternative interpretation would be that the conspicuous colorful plumage of a drake advertises its ability to evade predators. The ability to evade predators is meaningless on an island free of predators. The signal was therefore lost.

Another case may be that of the Satin bowerbird (*Ptilonorhynchus violaceus*). Adult males collect items to decorate their bowers, and prefer blue ones. They even steal such items from the bowers of their rival males. Dominant bower owners also destroy the bowers of their rivals (Borgia and Collins 1986). Hunter and Dwyer (1997) have found that near human habitation, where the number of blue items was artificially increased (drinking straws, bottle covers, cloth pegs, etc.), the number of such items collected was greatly increased. However, the rate of stealing was lower than in an undisturbed area, but the ratio of bower destruction relative to stealing increased.

The suggestion that signals would lose their function by a process of inflation can serve as a test for the theory that signals are selected by a different mechanism than all other characters, i.e. the mechanism of signal selection (Zahavi 1981).

5.6.1 The Interaction between Signal Selection and Utilitarian Selection

The notion that natural selection functions through two different selection mechanisms can explain the evolution of entirely new features, such as feathers (Zahavi 1981; Zahavi and Zahavi 1997). It is well established that feathers have evolved from reptilian scales. The function of a scale is to cover and protect the body. How can a well-adapted scale evolve into a feather, which is adapted for flight? It cannot change directly into a primitive feather by a series of additive mutations as each change will not be efficient — either for cover and protection, or for flight and will consequently be selected out by utilitarian selection. If, however, some scales evolved gradually to become signals to advertise certain traits, such as elegance of movement or certain jumps, then the scales may increase in size by the process of signal selection, handicapping their bearer's gait or jump, attesting to the reliability of the signal. Such scales can attain extravagant dimensions. The extravagant scales may then turn out to be of help in gliding. Once gliding becomes an important adaptation, the extravagant scales can evolve into utilitarian feathers by

utilitarian selection. I believe that over the millions of years of evolution by natural selection, a large number of innovative features became possible by the interplay of these two modes of selection: utilitarian selection and signal selection.

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Courtship and Copulation

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6.1 INTRODUCTION

Throughout recorded history, bird courtship behavior has been fascinating to humans. This may not be so surprising as, unlike those of many other animals, the displays of birds are performed mostly in the daytime, almost all of their display colors are within the human-visible spectrum, odors are rarely involved, and nearly all of the sounds that birds make are audible to humans. Moreover, many bird displays involve dancing, acrobatic movements and aerial maneuvers, all of which humans find enthralling.

Partly for these reasons, ornithologists have written a great deal about bird courtship, mainly describing displays and using them to inform phylogenetic analyses, to build theories about proximate motivation and drive, and, most recently, to examine their signaling function in an evolutionary context. Of course, Darwin (1871) was the first to examine bird courtship displays in the context of sexual selection—a concept that he formulated to explain the seemingly maladaptive behavioral and ornamental traits displayed by animals during the breeding season. For most of the next century, Darwin's ideas about sexual selection were largely ignored while biologists focused on traits relevant to survival and incorporated the emerging field of genetics into the study of evolution. It was not until the 1970s that serious attention was again devoted to courtship displays and ornaments, as well as copulation behavior, in the context of sexual selection. Some of this interest was kindled by the development of exciting new concepts with respect to sexual asymmetries in Parental investment (Chapter 9) sperm competition (Parker 1970; Volume 6A, Chapter 9) and honest advertisement (Zahavi 1975; Chapter 5).

Until the 1970s, there were three major trends in the study of avian courtship behavior. First, many authors compared the various apparently stereotyped courtship (and other) displays among closely related species to

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gain some insights into phylogenetic relationships. Some excellent studies of Anseriformes (Lorenz 1941) and Pelecaniformes (van Tets 1976) exemplify this approach. Second, the origins of courtship displays in some taxa were thoroughly studied—not evolutionary origins but rather how those displays were derived from other behaviors that the birds performed. This work was typical of mid-20th century ethology, inspired to a large degree by Niko Tinbergen (e.g., Tinbergen 1952), and resulting in detailed studies of motivation and the development of courtship behavior (e.g., Morris 1956). Books on courtship behavior by Armstrong (1947) and Bastock (1967) are excellent examples of this ethological approach. Finally, much attention was paid to the role of courtship as a species isolating mechanism. This focus grew out of the ‘new synthesis’ in evolutionary biology, bringing together ecology, behavior and genetics to understand the origin and maintenance of species (Mayr 1963). The key here was to understand how courtship behavior helped to maintain and reinforce species boundaries and minimize hybridization.

By the mid-1960s, evolutionary biologists in general (e.g., Williams 1966) and ornithologists in particular (e.g., Lack 1968) were turning their attention to the role of selection on individuals, marking the end of an era when behaviors were widely thought to evolve for the benefit of the species (when cooperation between the sexes was expected). Though there have been some excellent reviews of songs (e.g., Kroodsma and Miller 1996; Marler and Slabbekoorn 2004), colors (e.g., Hill and McGraw 2006), and sperm competition (e.g., Birkhead and Møller 1992) in birds from a modern evolutionary perspective, there has not been a complete review of bird courtship behavior since Armstrong (1947). Bird courtship does, however, figure prominently in more general works on sexual selection (Andersson 1994) and mating systems (Ligon 1999) and we refer the reader to these for both theoretical and empirical background.

In this chapter, we provide an overview of courtship and copulation behavior in birds in the context of modern behavioral and evolutionary ecology. This is a potentially vast topic so it is possible only to skim the surface in a review of this sort, particularly with respect to the behaviors, sounds, and ornaments used in courtship displays. Thus we have narrowed our focus to an evolutionary perspective on why and how birds court, and do not consider in detail most of the proximate mechanisms that influence courtship displays or the development of ornaments, some of which are dealt with in other chapters in this book (e.g., Chapters 1-5). Nor do we examine the evolutionary history of avian courtship behavior in relation to phylogeny, or the functional significance and ethological origins of different kinds of displays and ornaments. Instead, we have attempted to outline a number of hypotheses about courtship and copulation in an adaptive context to provide a focus for further study. To the best of our knowledge, this chapter presents the first attempt to review the various ultimate reasons why birds court. Several reviews have already done this for copulation behavior (e.g., Birkhead

et al. 1987; Birkhead and Møller 1992) and we update those here, adding examples and insights from the more recent literature.

6.1.1 Context

Courtship and copulation in birds are intimately related in that much of courtship behavior and associated sounds and ornamental traits seem to be designed to convince a member of the opposite sex to copulate. We consider courtship and copulation separately in this chapter because not all courtship—very little in fact—is followed immediately by copulation, and not all copulation—though most of it, at least when it is not forced—is preceded by courtship. Moreover, there is some reasonably convincing evidence that much of the courtship behavior of birds has nothing to do with copulation *per se*. In this chapter, we define courtship as the specialized signals (ornaments, sounds, displays) employed by one or both sexes that influence members of the opposite sex to engage in reproduction. We define copulation as the act of mounting, coitus (cloacal contact and, in some species, intromission), dismounting, and (sometimes) further display following coitus.

In addition to courtship, birds use signals during the reproductive period for both intrasexual interactions and mate attraction, both of which influence an individual's reproductive success. Typically, intrasexual interactions (usually male-male) are involved in the acquisition and defense of resources needed for breeding whether those resources are space, food, shelter, nest sites, or, eventually, mates. Once a territory or breeding site has been acquired and defended, different signals are sometimes used for mate attraction, though not always. In socially monogamous birds, for example, males typically establish and defend territories by both acoustic and physical displays directed towards neighbors and potential settlers. These songs and displays also attract females—potential mates—to the male's territory whereupon the male may employ different courtship songs and displays to encourage a female to stay, copulate, lay eggs and share the task of raising offspring.

In many bird species, there is little difference between the visual and auditory displays used in intrasexual competition, mate attraction and courtship, even though the displays used in these various contexts might differ in their general design rules and modality-specific mechanisms (compare Tables 18.1 and 18.3 in Bradbury and Vehrencamp 1998). In the American robin (*Turdus migratorius*), for example, males sing loud melodious songs from conspicuous perches during the period of territory establishment, before females even arrive on the breeding grounds, and these songs are clearly important in male-male interactions (Titus and Haas 1990). The songs continue after territory boundaries are established and females arrive, and presumably attract females to the male's territory. Males persist in singing at dawn after a female settles on their territory and it is quite possible that females use this male song to assess male quality and make decisions about copulation, particularly with respect to extrapair paternity which is high in this species (R. Montgomerie and P. Weatherhead, unpublished data). While

male robins do perform particular courtship displays immediately preceding copulation (Howell 1942; Young 1955), the dawn song that males perform every day during the period of territory defense, mate attraction, and female fertility is probably also a component of the courtship display as defined here. Because it is often difficult to distinguish among the different kinds of displays used in the context of reproduction in birds, we treat all of these displays under the rubric of 'courtship', although we focus primarily on displays that are clearly directed at members of the opposite sex.

In many ways, the intrasexual competition, mate attraction, courtship and copulation behaviors of individuals define their mating system. Though species have traditionally been classified as having a particular mating system (Lack 1968), the advent of both detailed study of color-marked individuals and DNA profiling have shown that, even within a single population, individuals can have a different mating tactic and the tactic that an individual uses can even vary among breeding episodes (Ligon 1999). Moreover, the social mating system, determined by observations, can be quite different from the sexual (genetic) mating system, revealed by maternity and paternity analyses based on DNA profiling (Griffith *et al.* 2002; Chapter 8). Thus, for example, within a single small marsh, there was little correspondence between the social and sexual mating tactics of both male and female Red-winged blackbirds (*Agelaius phoeniceus*), even though all males appeared to be socially polygynous and all females socially monogamous (Weatherhead *et al.* 1994). What this, and many other studies, have revealed is that courtship and copulation, and the success of both of these behaviors, have consequences both within and outside the social mating partnership in birds.

For general information on the sounds, displays and ornaments birds use while courting, we relied on major regional (e.g., Brown *et al.* 1982; Marchant and Higgins 1990; Cramp and Perrins 1994; Poole 2005) and global (Sibley and Ahlquist 1990; del Hoyo *et al.* 1992) treatises on birds, numerous field guides, and our own experiences with more than 500 species during the breeding season. In the interests of space and the flow of text, we do not refer to these references explicitly except when providing information or data on a particular species, and in those cases we refer only to the general reference and not the specific volume. Similarly, we refer to most bird families and orders by their common names as these should be familiar to most readers and can easily be looked up in any of the general references listed above.

6.2 COURTSHIP

Our approach in this section is to begin with a brief review of the various ornaments, sounds and displays associated with courtship in birds, including descriptions of the various morphological and behavioral traits associated with courtship and an overview of their taxonomic distribution. Then, we

review a number of hypotheses that have been proposed to explain the function of courtship in birds, outlining the general context in which each hypothesis is likely to pertain, an example of evidence consistent with the hypothesis, and some suggestions for further study.

Not all courtship traits function to attract mates or secure copulations, and this is reflected by the diversity of hypotheses proposed to explain the function and/or evolution of courtship displays and ornaments. The hypotheses we review also vary in scope from the proximate mechanisms guiding the evolution of courtship ornaments and behaviors, to the ultimate function of these traits. By their very nature, then, these hypotheses are not mutually exclusive and more than one may explain a particular courtship trait. Due to the breadth of this topic, we can only review each hypothesis briefly here, and we refer the reader to other chapters in this volume for further information.

6.2.1 Courtship Signal Design

Courtship signals may involve any of the four main sensory modes available to birds—auditory, visual, tactile, and olfactory—though olfactory (Chapter 3) and tactile signals appear to be rare. Many avian courtship signals rely on long-distance communication, perhaps by necessity or because these signaling modalities are well-developed in birds. Table 6.1 summarizes the properties of these four signal modalities with respect to signaling by birds. Because relatively little is known about how birds actually perceive signals, the signal properties that we have summarized in Table 6.1 are based on human perceptions and instrument measurements within the range of variation that we know birds can detect. Much more work is needed before we can be certain how birds actually perceive and respond to these signals.

Most mate attraction and courtship involves several traits and more than one sensory modality (Armstrong 1947), thus providing many signals to potential mates. The complexity of courtship displays surely reaches its peak in the manakins (Fig. 6.1E), bowerbirds (Fig. 6.2B), and birds of paradise, where various plumage colors, feather ornaments, vocalizations, dances, wing and tail motions, non-vocal sounds, and non-food objects (Fig. 6.2B) can all be employed by males courting females. It is probably no coincidence that most species in these families have a lek-based mating system (Frith and Beehler 1998; Frith and Frith 2004), where sexual selection is thought to be particularly intense (Andersson 1994).

Why are so many traits employed by a male when courting? It has been suggested that multiple traits might (i) provide some redundancy in the signaling system, (ii) amplify one another to provide an integrated signal, or (iii) signal different aspects of male (or female) quality (Candolin 2003). So far there is some empirical support for each these hypotheses (e.g., Doucet and Montgomerie 2003) but this is one (of many) aspects of courtship that deserve more study (Gil and Gahr 2002).

Table 6.1 Main features of signals used by birds during reproduction, including male-male interactions, mate attraction and courtship. Features listed here are based largely on human perception and measurement. Adapted from Bradbury and Vehrencamp (1998, Tables 18.1 and 18.3) and various general sources.

<i>Signal feature</i>	<i>Visual</i>	<i>Auditory</i>	<i>Olfactory</i>	<i>Tactile</i>
Prevalence in birds	nearly universal	nearly universal	very rare	uncommon
Potential range	very large (up to ≥ 1 km)	very large (up to ≥ 5 km)	very short (<1 m)	contact
Potential locatability	very high (both distance and direction)	high directionality and moderately high distance	low	highest
Degradation with distance	low	moderate to high depending upon environment	low	none
Species, sexual, and individual identity	very high via: 1. colors (hue, saturation, brightness) of plumage and bare parts 2. color patterns 3. displays	very high via: 1. vocal songs, calls 2. non-vocal sounds 3. repertoire size and syntax 4. note shape and pitch	possibly high via chemical differences	probably low but may be high if variation in pattern of contact via allogrooming, bill grasping
Interspecific variation	very high, virtually all species individually distinctive	very high, virtually all species individually distinctive	unknown (see Chapter 3)	low among closely related species
Intraspecific variation	moderate to high	high	presumably high (see Chapter 3)	unknown but probably low

6.2.2 Courtship Ornaments

In this section we provide a brief overview of the various ornaments that birds use during courtship displays. In the context of sexual selection, an ornament is any phenotypic trait that enhances mate acquisition but does not improve the survival of the bearer (and is thus usually not favored by natural selection). Typically, ornamental traits bear some cost so in fact reduce survival while enhancing reproductive success. Strictly speaking, then, the sounds and displays that are used in courtship are ornamental traits, but we deal with those separately in the next two sections, restricting our treatment here to colors, odors, structures and objects that comprise the phenotype and extended phenotype of courting birds.

Plumage colors. Coloration plays a critical role in avian courtship, with colors produced by the deposition of pigments into growing feathers (Chapter 2) or the physical interaction between light and nanostructural components of feathers (Chapter 1). Hill and McGraw (2006) provide an excellent review of the entire topic of color production, summarized briefly here.

The most common avian pigments are carotenoids (Figs. 6.1E and 6.2A), which produce red, orange, and yellow colors, and melanins (Figs. 6.1E and 6.2A), which produce blacks, browns, and grays. Psittacofulvins (Fig. 6.1G), porphyrins, and pterins are much rarer pigments, restricted to only a few taxa. Thus, psittacofulvins, rather than carotenoids, are responsible for producing red and yellow colors in parrots; porphyrins are reddish and green pigments in turacos as well as brownish pigments in owls, bustards, and goatsuckers; and pterins are yellowish and orangish pigments found in birds' retinas and almost certainly in some feathers.

Structural plumage colors are either (i) non-iridescent ultraviolet (Fig. 6.1F), violet, blue (Figs. 6.1E and 6.2E), turquoise, or green, produced by the coherent scattering of light within a keratin-air matrix in feather barbs, or (ii) iridescent, spanning the entire range of colors that birds can see, produced by laminar or crystal-like arrays of air, melanin, and keratin within feather barbules. These colors have not been as well studied as pigment-based colors but have received much attention recently (Chapter 1).

Feather structures. Various bird species grow feathers of such unusual shapes, colors, and sizes that they clearly serve functions beyond flight, camouflage, or insulation (Figs. 6.1 and 6.3-4), for which purposes they might even be detrimental (Darwin 1871). Because these unusual feathers often grow only in the breeding season, they are almost certainly courtship traits.

Elongated tail feathers are among the most common feather ornaments, occurring in a broad diversity of taxa (Fig. 6.3). Possible reasons for their widespread occurrence as ornaments include pre-existing female preferences for long tails (Pryke and Andersson 2002), a lower cost to flight performance of ornamental tail feather modification than wing feather modification



CMYK



Fig. 6.1 Some feather structures and colors presumed to be used in courtship and mate attraction. **A.** Erectile crown feathers of male Royal flycatcher **B.** Erectile crest of male Barred antshrike (*Thamnophilus doliatus*) **C.** Large, colorful beak of both

Fig. 6.1 Contd. ...



KMYC



(Norberg 1995), and the potential for natural selection to initially favor some tail lengthening (Rowe *et al.* 2001).

In addition, the shape, color, and display of birds' tails vary both in combination with, or independent of, lengthening. For example, tails can be forked (e.g., swallows: Fig. 6.3E), graduated (e.g., doves, hummingbirds, grouse; Fig. 6.7A,B), or pin-shaped (e.g., manakins, lyrebirds, birds of paradise; Fig. 6.3A,F), and individual feathers can be narrowed (e.g., tyrants, snipe; Fig. 6.7D), wiry (e.g., swallows, manakins, lyrebirds, birds-of-paradise; Figs. 6.3A,E,F and 6.4C), pointed (e.g., hummingbirds, pheasants, grouse; Figs. 6.6E and 6.7B), or racqueted (e.g., motmots, kingfishers, hummingbirds; Fig. 6.3B-D). Many species cock their tails during courtship (e.g., wrens, fairy-wrens, grouse, sandpipers; Figs. 6.6E and 6.8B), while others wag their tails (e.g., motmots), or lift and spread them in a fan (e.g., grouse, peafowl, lyrebirds; Figs. 6.3F and 6.8F).

Modified crown, facial, and neck feathers are also a common type of ornamental feathers in birds (Figs. 6.1A,B, 6.4, and 6.7E). In many birds, the crown feather are elongated, giving rise to a prominent crest that can be permanently erect (e.g., waxwings, quail, auklets; Figs. 6.4D and 6.7E) or erected only during courtship and agonistic displays (e.g., Figs. 6.1A,B, 6.4A,C,F, 6.6E and 6.7A). Other ornamental feather types used in courtship tend to be restricted to only a few species, like the elaborate neck feathers found in the coquette hummingbirds (genus *Lophornis*) and the Tui (*Prothemadera novaeseelandiae*; Fig. 6.4B), the elongated wing streamers of the Pennant-winged nightjar (*Macrodipteryx vexillarius*; Fig. 6.3G), and the remarkable modifications of various types of contour feathers in birds-of-paradise (Frith and Beehler 1998; Figs. 6.3A and 6.4C).

Feathers that exhibit these conspicuous structural modifications are often strikingly colored or patterned (Figs. 6.1A,B and 6.4B,E). Similarly, brightly colored feathers often exhibit microscopic modifications that enhance their colorful signals, such as flattened barbules on iridescent feathers (Osorio and Ham 2002), or both a flattening of the barbs and a reduction in the number of barbules in feathers with non-iridescent, structural colors (Shawkey *et al.* 2005).

Fig. 6.1 Contd. ...

sexes of Atlantic puffin (*Fratercula arctica*) in breeding season **D**. Bright red supraorbital combs of male Rock ptarmigan (*Lagopus mutus*) raised during courtship and male-male aggression by engorging with blood; otherwise hidden below crown feathers; much reduced in non-breeding season **E**. Carotenoid (red crown), melanin (black body), and structural (blue back) plumage colors of the male Long-tailed manakin (*Chiroxiphia linearis*) **F**. UV-reflecting structural plumage color of the male Satin bowerbird (*Ptilonorhynchus violaceus*) **G**. Plumage colors of male King parrot (*Alisterus scapularis*) due to red psittacofulvins (head and breast) and a combination of yellow psittacofulvins and blue structural color producing the green of the back and wings. Original photographs by S. Doucet (A,B,E), R. Montgomerie (C,D,G), and Dan Mennill (F).



C M Y K



Fig. 6.2 Some examples of courtship and copulation. **A.** Male Red-winged blackbird 'Song Spread' display; the most common display given by territorial males during the breeding season **B.** Satin bowerbird male standing on bower platform that he has decorated with blue feathers, with bower behind him **C.** Common goldeneye female initiating copulation sequence by stretching out head and neck on water **D.** Herring gulls (*Larus argentatus*) copulating **E.** Tree swallows copulating. Original photographs by P.-G. Bentz (A,E) and R. Montgomerie (B,C,D).



K M C



Bare part colors and structures. In addition to colorful and ornamented feathers, birds also often display colorful bare parts such as patches of skin (e.g., vultures, guineafowl, antbirds, Australian honeyeaters, asities; Figs. 6.4E and 6.5D), as well as snoods (e.g., turkeys, Fig. 6.6D), combs (e.g., grouse; Figs. 6.1D, 6.6B,E and 6.8F), wattles (e.g., junglefowl, bellbirds; Figs. 6.5C,E and 6.6C), esophageal sacs (e.g., grouse; Fig. 6.6E), expandable lappets (e.g., tragopans; Fig. 6.6A), gular sacs (e.g., frigatebirds), casques (e.g., cassowaries), and brightly colored and/or unusually shaped bills (e.g., puffins, toucans; Figs. 6.1C and 6.5A,B,D). The color-production mechanisms for these ornaments are often the same as those responsible for coloring feathers. For example, colorful ultraviolet, blue, green, orange, and yellow skin patches are produced structurally through the coherent scattering of light by dermal collagen arrays or by a combination of structural mechanisms and pigments (Hill and McGraw 2006). Similarly, carotenoids are responsible for creating yellow, orange, and red skin and bill coloration in many species (Hill and McGraw 2006), though care should be taken not to infer probable mechanisms of coloration based on appearance alone. For example, the red coloration of wattles and combs in many species is probably strongly influenced by the presence of hemoglobin in the blood that engorges these structures rather than pigments (Hill and McGraw 2006).

Odors. Although birds are not particularly well-known for their sense of smell, early views that many birds had at best a limited sense of smell are called into question by recent findings (Chapter 3). Crested auklets (*Aethia cristatella*), for example, have a tangerine-scented odor that likely functions in mate choice (Fig. 6.7E; Chapter 3).

Food (courtship feeding). In many species of birds, food offerings form part of the courtship display, most often performed by males, and most common in species that form stable pairs during the breeding season (Lack 1940; Smith 1980; Fig. 6.8C). Typically, courtship feeding begins when courtship commences and extends through to the period of egg laying (Fig. 6.9A,C). While it can clearly serve a nutritional function, enhancing the female's ability to lay more and better quality eggs (Davis and Graham 1991; Helfenstein *et al.* 2003), courtship feeding has also been shown to be related to copulation rate in the Osprey (*Pandion haliaetus*; Fig. 6.9B), suggesting that females may use it as a signal of male quality (Mougeot *et al.* 2002).

Non-food objects. The best-documented examples of the use of non-food objects during courtship are the petal-carrying behavior of males in many species of fairy-wren (Rowley and Russell 1997) and the collection, arrangement, and display of natural and human-manufactured decorations in bowerbirds (Frith and Frith 2004; Figs. 6.2B and 6.8G). In some species, the gathering of nesting material also appears to function as a courtship display (e.g., Marsh wren, *Cistothorus palustris*; Metz 1991).

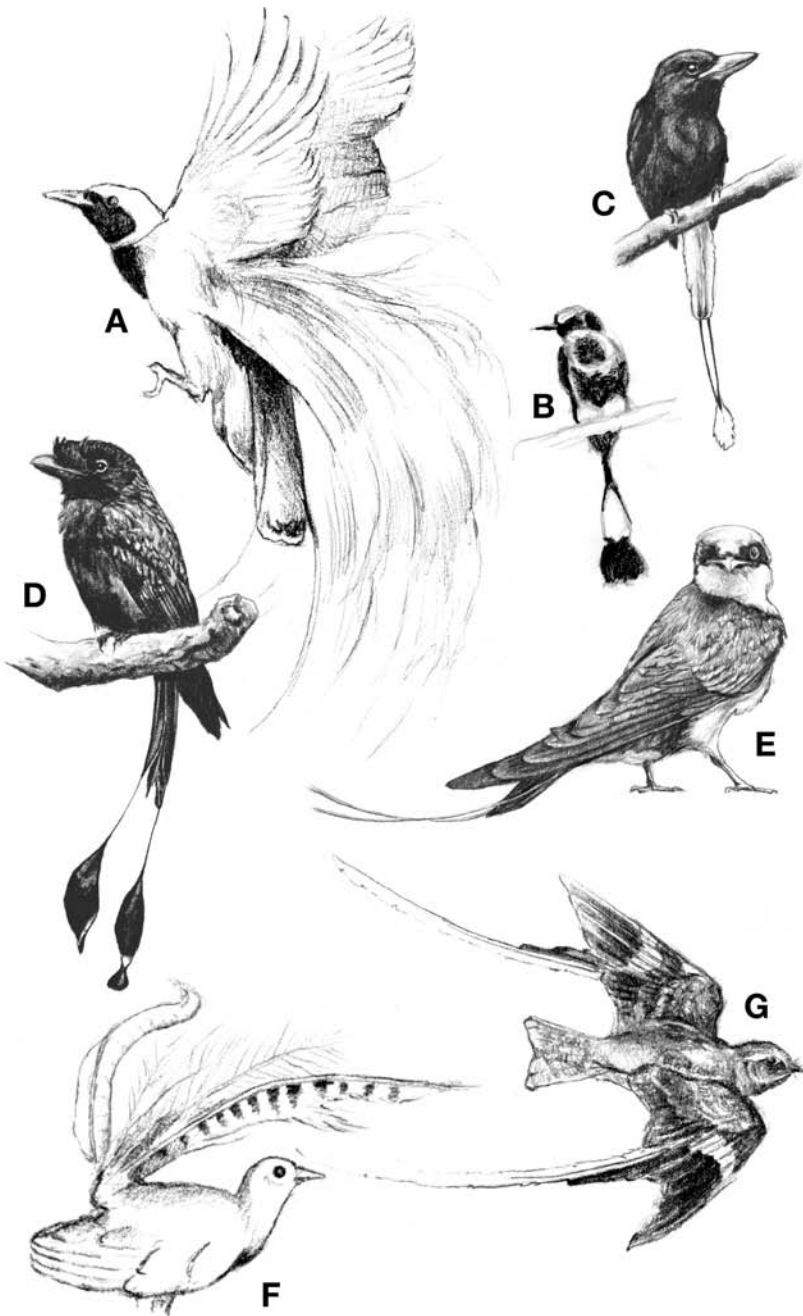


Fig. 6.3 Some examples of interesting tail feather ornaments presumed to be favored by sexual selection in birds. **A.** Male Raggiana bird-of-paradise

Fig. 6.3 Contd. ...

6.2.3 Courtship Sounds

The songs produced by (mostly male) birds during the breeding season are probably the most diverse, conspicuous, and beautiful sounds in the animal kingdom. Several excellent treatises on bird song have been published over the past 25 years (e.g., Kroodsma and Miller 1982, 1996; Catchpole and Slater 1995; Bradbury and Vehrencamp 1998; Marler and Slabekoorn 2004; McGregor 2005; Kroodsma 2005), and we refer the reader to these books for a comprehensive treatment of the subject. In this section, we summarize the types of sounds that birds make during the breeding season in the context of mate attraction and courtship. Then, we provide a brief overview of both the main factors responsible for interspecific variation and some of the ways that sexual selection appears to influence intraspecific variation in bird song.

6.2.3.1 Types of sounds

Vocalizations. Birds produce diverse sounds ranging from the unusual clicking sounds produced by swifts, to the melodious songs of thrushes, and the remarkable vocal displays of oropendolas. All birds vocalize, although some species (e.g., vultures) produce only occasional hisses and grunts.

Although avian vocalizations can serve many functions, most birds clearly use at least some of their vocalizations during courtship (Figs. 6.2A, 6.3F, 6.6E and 6.8B,D,E,F. In many songbirds, learned vocalizations are sung only by males and almost exclusively during the breeding season. Bird song is often assumed to serve both an intersexual, mate attraction function, and an intrasexual, territorial advertisement, function (Fig. 6.2A). In the North American wood warblers (family Parulidae), males appear to use different song types in these different contexts (e.g., Fig. 6.10), but in most other species the same songs are used in both circumstances. In some species both males and females sing during courtship and, in some of these, males and females

Fig. 6.3 Contd. ...

(*Paradisaea raggiana*): long-tapering, yellow, filamentous flank plumes; elongated wire-like central tail feathers **B**. Male Booted racquet-tail (*Ocreatus underwoodii*): white leg puffs; outer tail feathers with blue-black racquets at tips of bare shafts **C**. Both sexes of Numfor paradise-kingfisher (*Tanysiptera carolinae*): central tail feathers with bare blue shafts and white spatulate tips **D**. Male Greater racquet-tailed drongo (*Dicrurus paradiseus*): wire-like extensions of central tail feathers end in elongated, twisted racquets **E**. Male Wire-tailed swallow (*Hirundo smithii*): outer tail feathers (streamers) elongated with wire-like filaments **F**. Male Superb lyrebird: wire-like central tail feathers; lyre-shaped broad outer tail feathers; all other tail feathers filamentous; while courting male fans and quivers tail in wide arc over back, imitates sounds and songs of other birds, hops side-to-side and leaps in air **G**. Male Pennant-winged nightjar: elongated innermost primaries displayed in leks, in flight or on ground. Original drawings by Kevin Fraser.

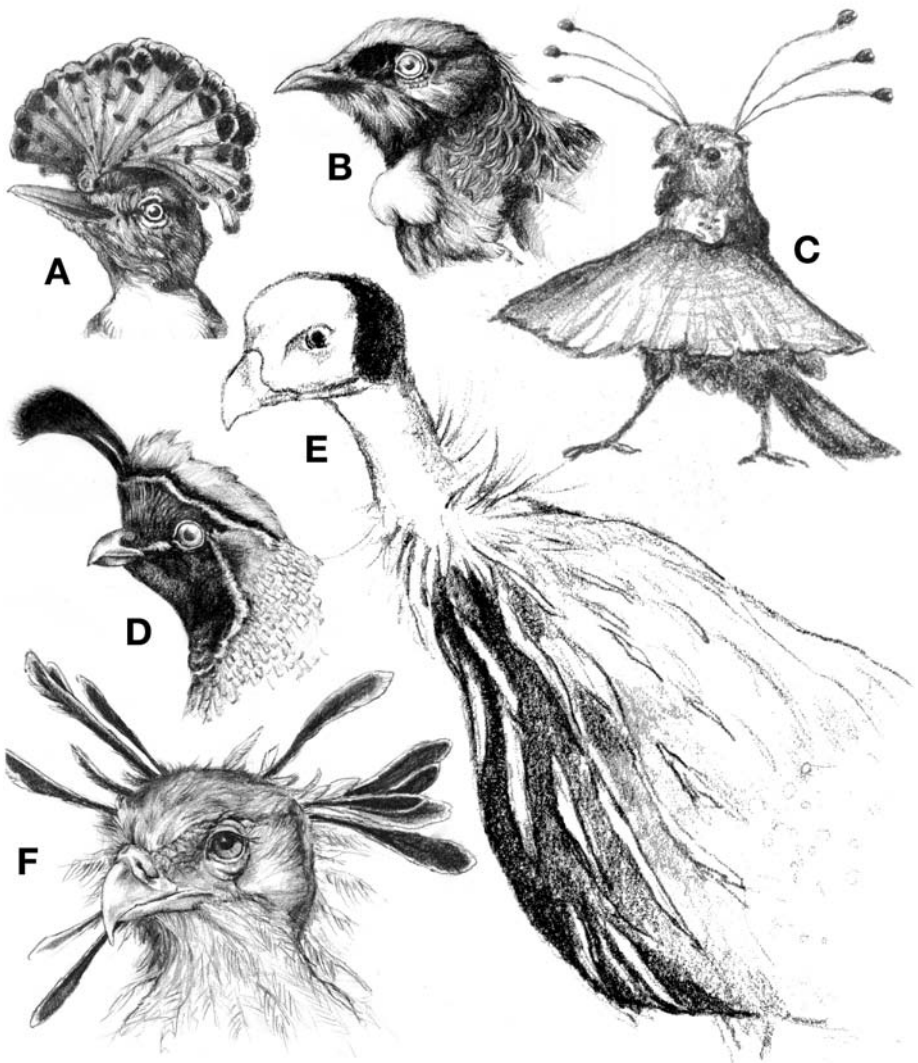


Fig. 6.4 Some examples of interesting head and body feather ornaments presumed to be favored by sexual selection in birds. **A.** Male Royal flycatcher (*Onychorhynchus coronatus*): crown fan of vermillion feathers (orange or yellow in female) tipped with blue; usually hidden but when raised is perpendicular to long axis of head as shown here **B.** Both sexes of Tui: small, pointed, curved, blue-black feathers with white shafts on nape, extending to sides of head and mantle; one ball-like white tuft on each side of throat, composed of about 20 white feathers that have reduced barbules and curl together to form ball **C.** Male Western parotia (*Parotia sefilata*): behind each eye, 3 long, erectile, wire-like plumes with circular flag at tip (erected during courtship but otherwise lie down back); bronze iridescent

join their songs into coordinated vocal duets (Hall 2004; Mennill and Vehrencamp 2005).

Non-vocal sounds. Birds also produce a wide variety of non-vocal sounds during courtship. In many species, wing or tail feathers are structurally modified such that they produce (i) whistled sounds during display flights (e.g., ducks, hummingbirds, manakins, snipes; Fig. 6.7B,D), (ii) snapping, cracking and drumming sounds (e.g., manakins, doves, grouse; Fig. 6.7A), and (iii) high-pitched whines when feathers are rubbed together (e.g., manakins). In some species of grouse, waders, and bitterns, males also have esophageal air sacs that are inflated during courtship (Fig. 6.6E) and amplify the sounds produced by the syrinx. Many woodpeckers (Fig. 6.7C) and other birds make special sounds during courtship by striking other objects with their bills or feet.

6.2.3.2 Interspecific variation

While there is an incredible diversity of sounds made by birds, both within and outside the breeding season, the frequencies of bird sounds all appear to fall almost entirely within the normal range of human hearing (20-20,000 Hz), and mostly within 1-4 kHz. A few species have been recorded making sounds near the lower and upper limits of human hearing but these are relatively rare. Because a large body size is needed for a bird to make loud sounds at low frequency, it is not surprising that large-bodied birds have been recorded making the lowest sounds, close to the infrasonic range (Moss and Lockie 1979; Mack and Jones 2003). Cassowaries (family Casuariidae), for example, make a series of pulsed booming sounds as low as 23 Hz (Fig. 6.11A; Mack and Jones 2003). Such low-frequency sounds travel large distances with little attenuation in forest environments. At the other end of the scale, very few species make sounds above 10 kHz, well below the upper limit of human hearing. Among North American birds, the highest frequency songs are found among the sparrows and warblers with the highest frequency songs found in the Blackpoll warbler (*Dendroica striata*) whose peak frequencies reach barely into the 10-11 KHz range (Fig. 6.11B).

In addition to variation in the frequencies encompassed by bird song, there is incredible diversity in the structure of song syllables, the duration of songs

Fig. 6.4 Contd. ...

throat feathers; elongate flank feathers erected to form skirt during 'Ballerina Dance' (shown here) as part of complex courtship display; male performs dance on ground below females watching from vegetation above, sometimes holding flags almost stationary while moving head side-to-side below flags **D**. Male Gambel's quail (*Callipepla gambelli*): forehead plume (smaller in females) **E**. Both sexes of Vulturine guineafowl (*Acryllium vulturinum*): long black and white feathers (hackles) on lower neck **F**. Both sexes of Secretarybird (*Sagittarius serpentarius*): elongate, spatulate nape feathers, raised (as shown here) or lowered along neck; bright orange facial skin. Original drawings by Kevin Fraser.

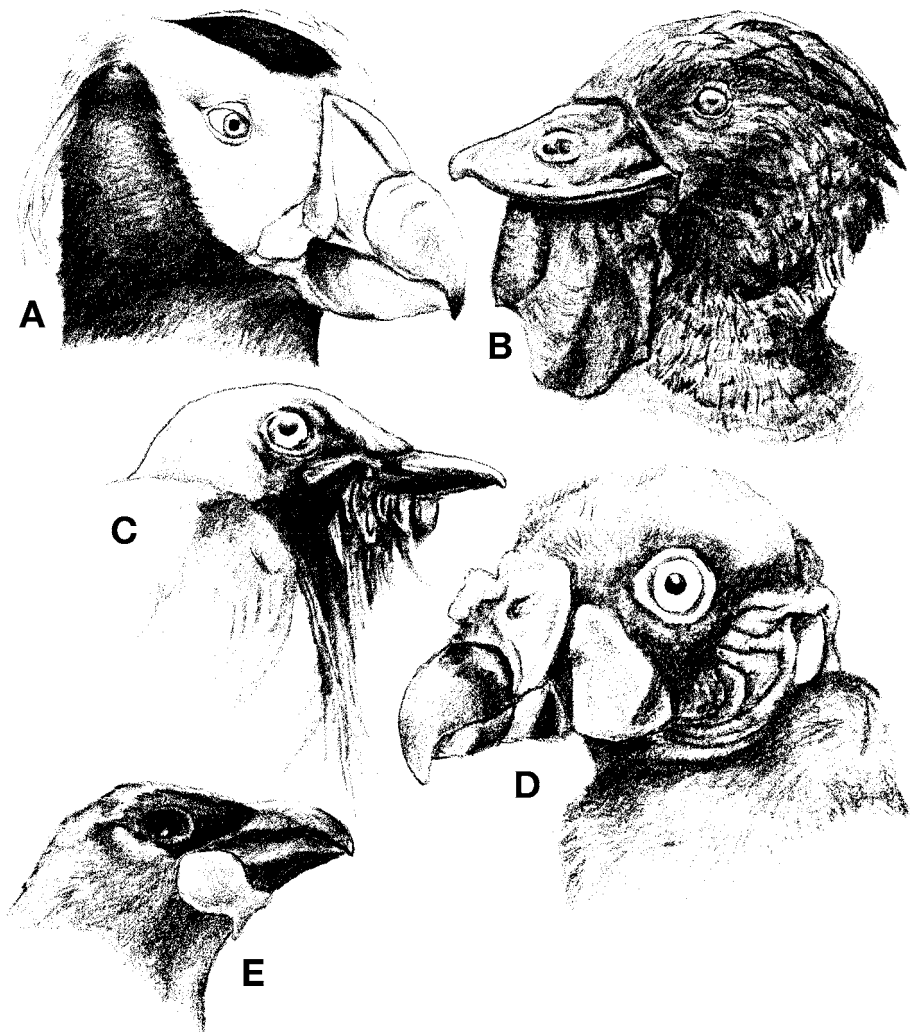


Fig. 6.5 Some examples of interesting bill and bare part ornaments presumed to be favored by sexual selection in birds. **A.** Both sexes of Tufted puffin (*Fatercula cirrhata*): huge salmon-red and olive bill plates, and long golden head plumes; only during breeding season **B.** Male Musk duck (*Biziura lobata*): distensible gular skin below bill (smaller in female), inflated during courtship display (shown flaccid here) **C.** Male Bearded bellbird (*Procnis averano*): throat entirely covered with extensible, fine black wattles **D.** Both sexes of King vulture (*Sarcorhamphus papa*): bright orange neck, yellow throat, purple head, and red crown skin; head skin folded into complex corrugations; white eye surrounded by bright red sclera **E.** Both sexes of Kokako (*Calleas cinerea*): disk-shaped blue, orange or yellow wattles (color varies with subspecies). Original drawings by Kevin Fraser.

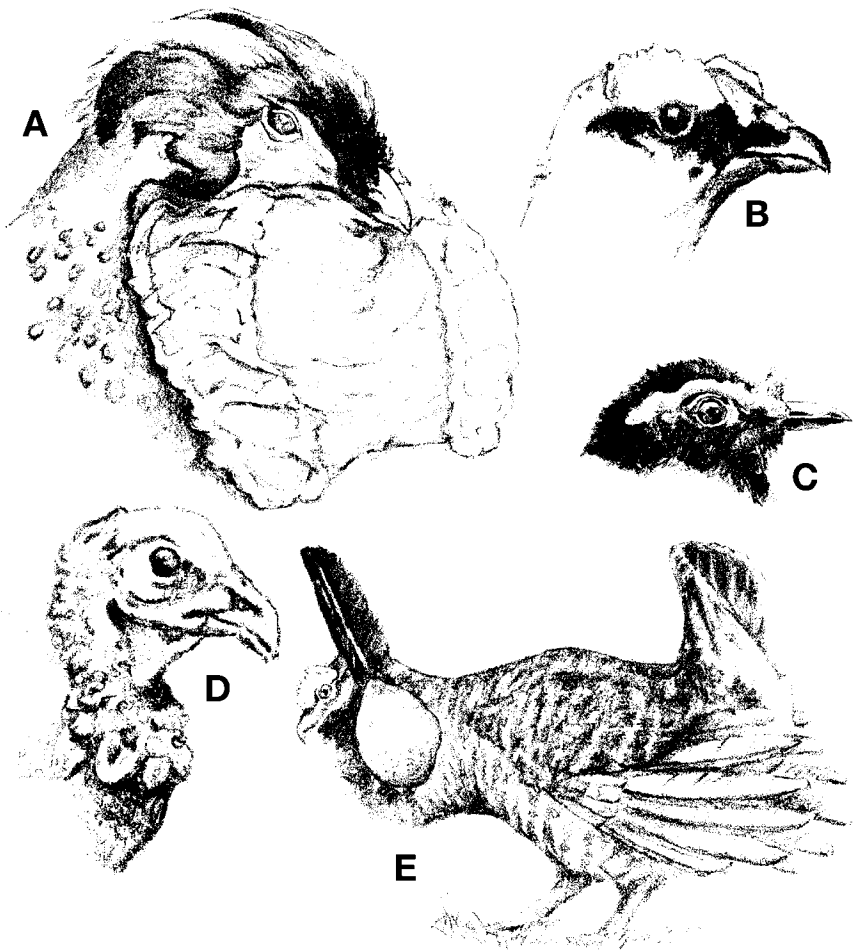


Fig. 6.6 Some examples of interesting bare part ornaments presumed to be favored by sexual selection in birds. **A.** Male Temminck's tragopan (*Tragopan temminckii*): dark blue and scarlet chest skin (lappet), inflated and exposed across breast during courtship when male holds upright posture in front of female; lappet deflated and hidden by breast feathers outside courtship display; at height of display male raises two fleshy blue horns on head (hidden beneath crown feathers here) **B.** Male Rock ptarmigan with raised supraorbital combs **C.** Male Velvet asity (*Philepitta castanea*): vivid green wattle over eye and horn over base of bill during breeding season; inflated during courtship display; wattle has narrow bright blue line over eye **D.** Male Wild turkey (*Meleagris gallopavo*): bare red head with caruncles and flap of skin (snood) hanging down from bill, as well as a beard of keratinous fibers hanging down from midline of breast; only in breeding season **E.** Male Greater prairie chicken (*Tympanuchus cupido*): orange esophageal air sacs, edged with scarlet, and orange superciliary combs; air sacs usually hidden by neck feathers but during 'Booming Display' (shown here) inflated and used to amplify three-syllable booming sound produced by syrinx. Original drawings by Kevin Fraser.

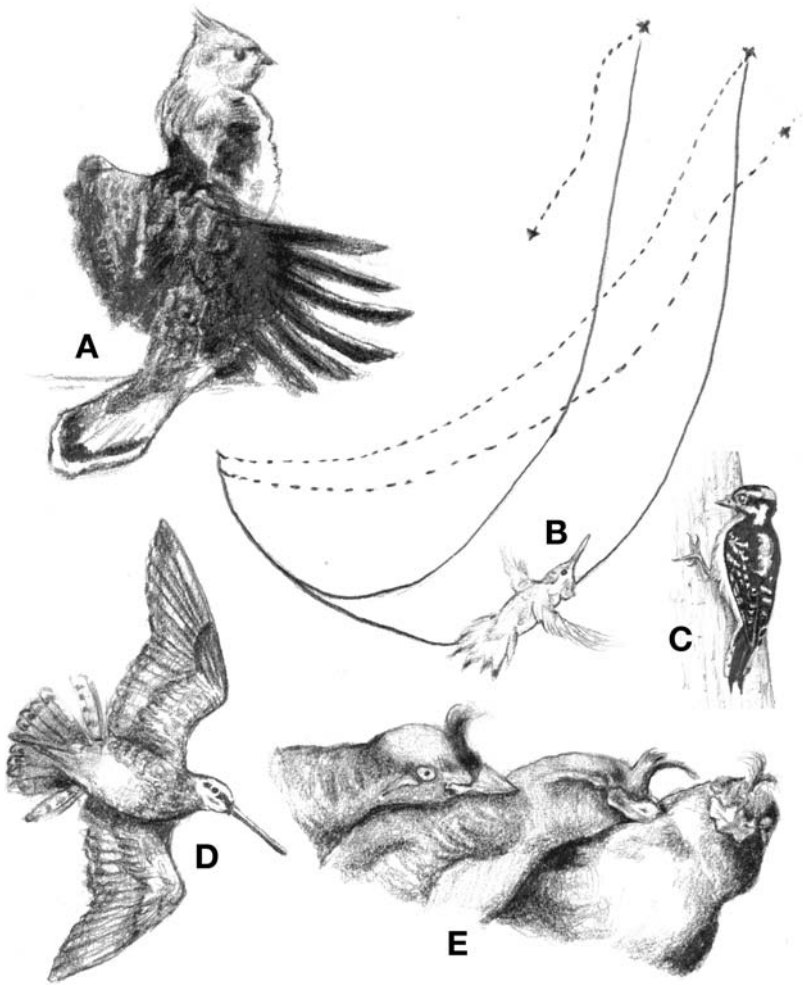


Fig. 6.7 Some examples of interesting sounds and odors used in courtship by birds. **A.** Male Ruffed grouse (*Bonasa umbellus*): drumming by flapping wings toward breast, while holding log with claws and bracing tail to stay upright; drumming sound produced by air rushing in as wings pulled rapidly away from breast; performed during spring courtship on fallen log in male's territory **B.** Male Rufous hummingbird (*Selasphorus rufus*): courtship flight over perched female; male actively flies to apex, then dives and levels out over female producing whistles and pops with his tail feathers **C.** Both sexes of Downy woodpecker (*Picoides pubescens*): steady staccato drumming on hollow tree, mainly in breeding season **D.** Male Wilson's snipe (*Gallinago delicata*): winnowing sound during aerial display produced by wind rushing over modified outer tail feathers held at particular angle, modulated by beating of the wings **E.** Both sexes of Crested auklet: smelling tangerine-like odor on nape during 'ruff sniff' courtship display (group display shown here). Original drawings by Kevin Fraser.

and inter-song intervals, as well as song continuity, versatility, and rate (e.g., Read and Weary 1992), all of which can readily be distinguished by human observers and are presumed to be important signals to birds. Songs are composed of syllables (or notes, or elements; e.g., A, B, C, D, etc.) that can be readily distinguished from one another by ear or by eye on a sonogram (e.g., Fig. 6.11C), and are separated from other such syllables by at least a short period of silence. Thus syllables are defined somewhat subjectively and the classification of syllables is somewhat observer-dependent. Nonetheless a bird's song repertoire size is usually measured as the total number of syllable types or song types sung by an individual (Catchpole and Slater 1995). The song repertoires of individual birds rarely exceeds 30-40 distinctive syllables (Wiley 2000), regardless of observer biases. The record song repertoire size is probably held by a single male Brown thrasher (*Toxostoma rufum*), a species in the family Mimidae (see Vocal mimicry below), who sang more than 2000 distinct syllables during a single breeding season (Kroodsma and Parker 1977).

In most species, like the American robin, each male in a local neighborhood has an individually distinctive song repertoire (15-35 notes) that, like a fingerprint, can be used to identify the bird from all others in the neighborhood, and possibly even from all other males in the entire population or species (Fig. 6.11C; R. Montgomerie unpublished data). At the other extreme, the majority of male Lapland longspurs (*Calcarius lapponicus*) in a neighborhood sing exactly the same repertoire of a single song type composed of 15-20 distinct syllables (Fig. 6.11D) always presented in the same order, making most males in a neighborhood virtually indistinguishable from one another by their songs (Mullie 1991; Hussell and Montgomerie 2002). Sometimes, as in the American robin, these repertoires gradually change and become larger as the male ages and gains more experience, whereas in others, like the Lapland longspur, the repertoire, and thus the 'song' remains the same throughout the bird's life (R. Montgomerie unpublished data). Literally dozens of excellent studies have documented both of these patterns in a wide variety of species (for reviews see Kroodsma and Miller 1982, 1996; Catchpole and Slater 1995; Marler and Slabbekoorn 2004).

Birds sing their song repertoires with immediate versatility (e.g., ABDCDCACBA; Fig. 6.11C), eventual versatility (e.g., AAAADDDDDCCB), or no versatility (e.g.,BBBBBBB; Fig. 6.11D) during each bout of singing. In a survey of European and North American songbird species, for example, Read and Weary (1992) classified species as singing with immediate ($n = 35$), eventual ($n = 44$) or no ($n = 29$) versatility. Moreover, syllables are often strung together in specific sequences classified as different song types, so another way to examine song diversity is to enumerate the number of different song types that an individual or species sings. In some species, different song types are used in different contexts, whereas in others the variety of song types merely contributes to signal diversity in a single context. In the American

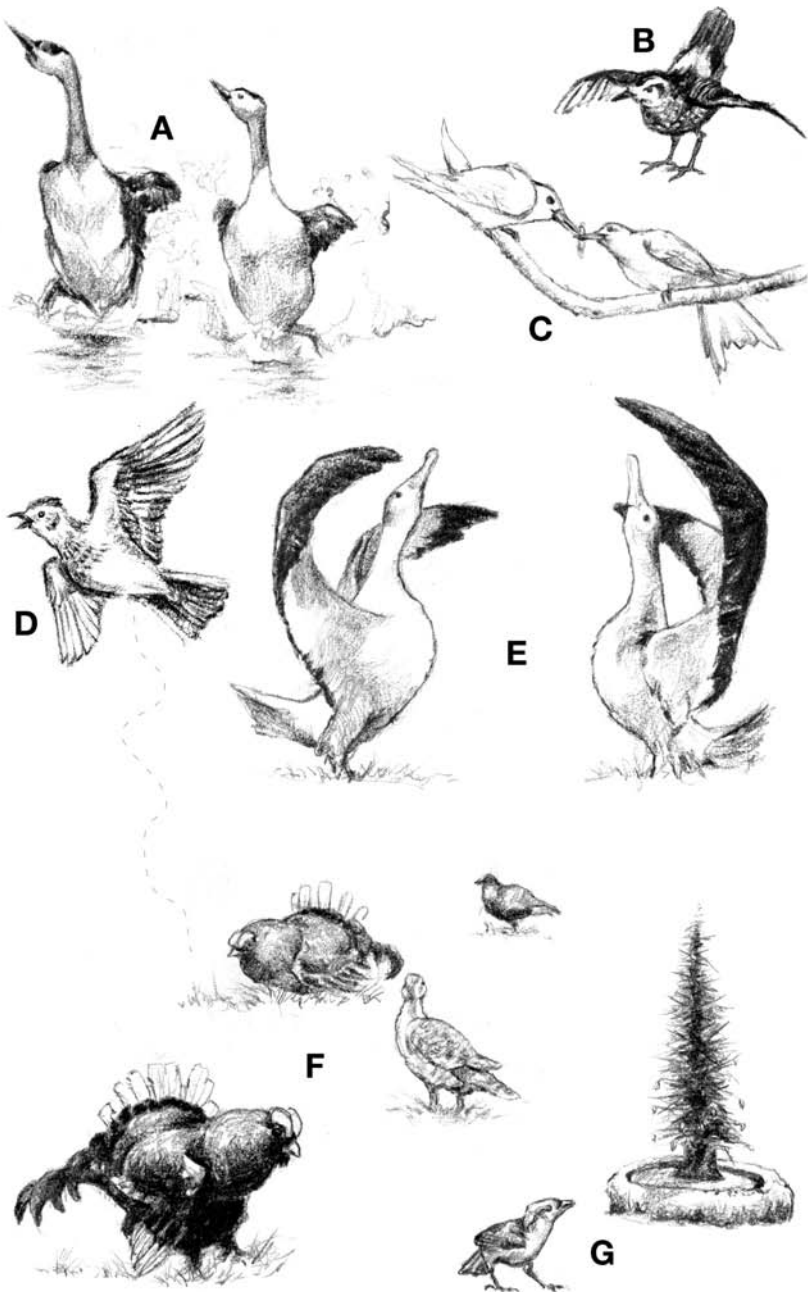


Fig. 6.8 Some examples of interesting courtship behaviors in birds. **A.** Both sexes of Western grebe (*Aechmophorus occidentalis*): 'Rushing Ceremony' involving

Fig. 6.8 Contd. ...

redstart (*Setophaga ruticilla*; family Parulidae), for example, males sing a 'serial song' when interacting with other males over territory and a 'repeat song' at the time of mate acquisition (Fig. 6.10; Lemon *et al.* 1987). Interestingly, most male redstarts retain the same repeat song from one year to the next, but their serial song repertoire changes between years (Lemon *et al.* 1994), possibly the opposite of what might have been expected if repeat songs honestly advertise age and experience to potential mates.

Why is there variation in the size, complexity, individual distinctiveness, and ontogeny of avian song repertoires? The tremendous variety of bird sounds made during the breeding season can largely be attributed to phylogeny, environment, anatomy, and sexual selection. As any good birder can attest, closely-related species tend to make similar, though species-specific, sounds. Some of this similarity between closely-related species is due to similarities in body size, which influence the minimum frequencies for loud sounds in birds, as mentioned above. Nonetheless there appears to be considerable phylogenetic inertia in the evolution of birdsong (e.g., van Buskirk 1997), with the remaining differences between species resulting from genetic and cultural drift, natural selection and sexual selection. Because even very closely related species (e.g., Stein 1963; Kroodsma 1984), as well as allopatric populations within some species (e.g., MacDougall-Shackleton and MacDougall-Shackleton 2001), have songs that are distinctive to the human ear, it has been suggested that songs may be an important part of the species recognition, speciation and species isolation processes (Baptista and Trail 1992; Slabekoorn and Smith 2002).

The environment also appears to be an important factor influencing many characteristics of bird sounds. Birds breeding in open habitats are more likely to make high pitched sounds as these do not attenuate (degrade) as much unless it is windy. In forest environments, lower frequency sounds are

Fig. 6.8 Contd. ...

mated pair running across water surface, then diving synchronously **B.** Male White-rumped sandpiper: grouse dance performed on ground in front of female; also performs aerial displays **C.** Fairy tern (*Gygis alba*): male brings small fish to female as part of courtship **D.** Male Eurasian skylark (*Alauda arvensis*): song flight; rises diagonally into wind, with tail spread and wings fluttering, to 100 m or more above ground, then hovers 1-10 min before gliding downward in spiral, then folds wings and plummets to earth **E.** Both sexes of Wandering albatross (*Diomedea exulans*): 'Ecstatic Ritual' performed on nesting grounds before egg-laying begins; at end of display, birds give loud, braying whistle followed by inhaled sigh **F.** Male Black grouse (*Tetrao tetrix*): displaying on leks of up to 50 males dancing and calling; females visit leks often but usually copulate with only one male; 3 males and a female shown here **G.** Male MacGregor's bowerbird (*Amblyornis macgregoriae*): male builds and displays at maypole bower consisting of a conical tower of sticks around 1-5 m tall sapling, surrounded at base by circular moss mat with raised rim; during courtship male and female walk around bower. Original drawings by Kevin Fraser.

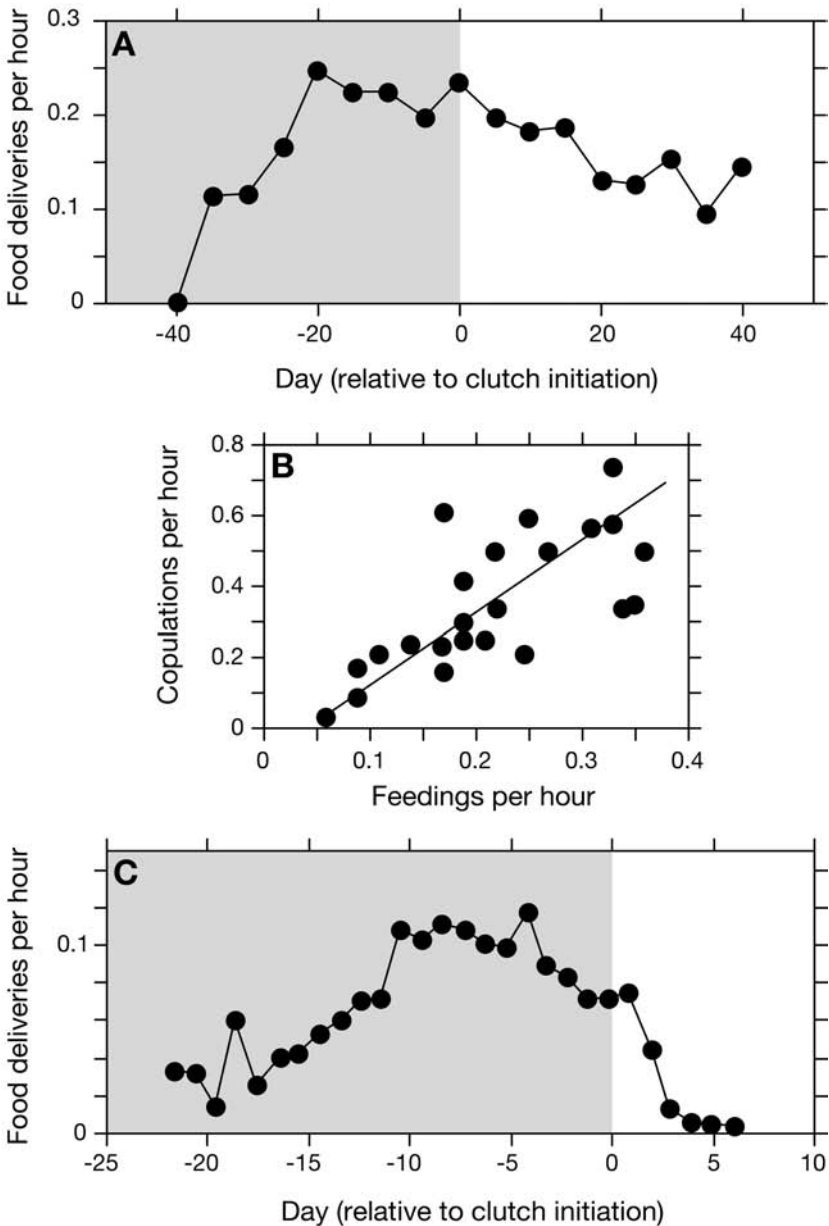


Fig. 6.9 Courtship feeding. **A-B.** Osprey: seasonal pattern (A), and relation between copulation rate and courtship feedings (B; $r = 0.70$, $P = 0.0002$, $n = 23$). Modified after Mougeot, F., Thibault, J.-C. and Bretagnolle, V. 2002. *Animal Behaviour* 64: 759-769, Figs. 1b and 2. **C.** Black-legged kittiwake: seasonal pattern. Modified after Helfenstein, F., Wagner, R. H., Danchin, E. and Rossi, J. M. 2003. *Animal Behaviour* 65: 1027-1033, Fig. 1.

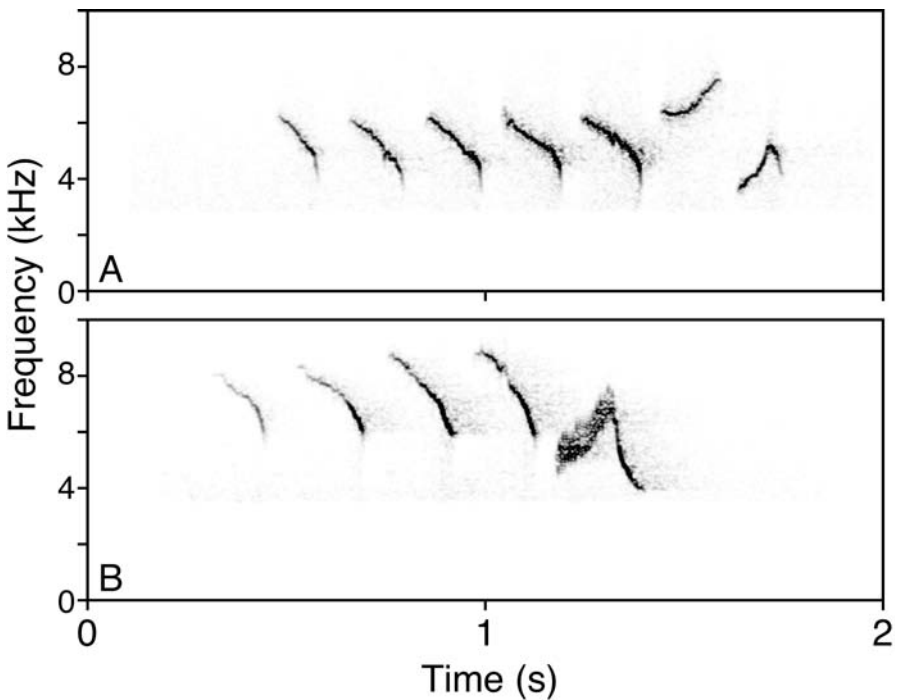


Fig. 6.10 Different song types used by male American redstarts during **A.** Inter- and **B.** Intrasexual encounters. Original recordings and sonograms by Dan Mennill.

expected since these are less attenuated by transmission through the foliage. Morton (1975), for example, found that sounds in the 1.6–2.5 KHz range traveled best through woodland, though this may only be significant for species that sing near the ground (Marten *et al.* 1977). In the North American wood warblers, song structure is correlated with habitat features (Fig. 6.12) though the notes (syllables) that comprise their songs are better predicted by each species' phylogenetic history (van Buskirk 1997). We refer the reader to the extensive birdsong literature (e.g., Read and Weary 1992; Catchpole and Slater 1995; Marler and Slabekoorn 2004) for some additional insights on the differences between species repertoires related to the environment.

The timing of the dawn chorus also varies interspecifically (Allen 1913), but the causes of this variation are only beginning to be understood. A recent study has shown that the timing of the dawn chorus song of passerine birds in a tropical forest in Ecuador is best predicted by foraging height, with canopy birds singing earlier than birds that forage closer to the ground (Fig. 6.13B; Berg *et al.* 2006). Because light attenuation through the foliage is also related to height above the ground, Berg *et al.* (2006) interpreted this pattern as evidence in favor of the inefficient foraging hypothesis (see 6.2.3.3, Intraspecific variation: Dawn chorus below) since many of these species are

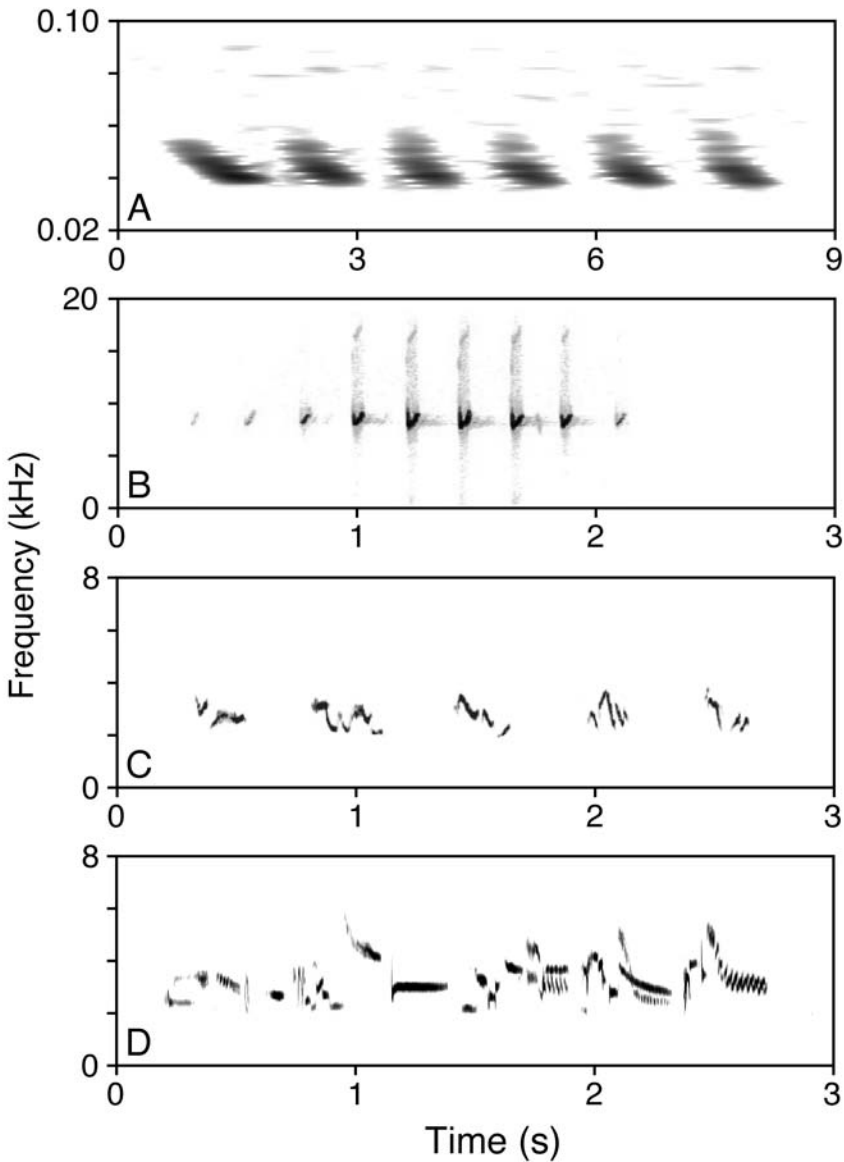


Fig. 6.11 Sonograms of songs performed in the breeding season by male **A.** Cassowary (*Casuarus casuarus*), **B.** Blackpoll warbler, **C.** American robin, and **D.** Lapland longspur. A modified after Mack, A. L. and Jones, J. 2003. Auk 120: 1062-1068, Fig. 1A; B-D original sonograms from recordings by R. Montgomerie.

insectivorous and prey capture would improve as light levels increase. But why is there a dawn chorus in the first place? Is it just an epiphenomenon of selection on another aspect of avian activities, or is it influenced by sexual selection (see Section 6.2.3.3 Intraspecific variation)?

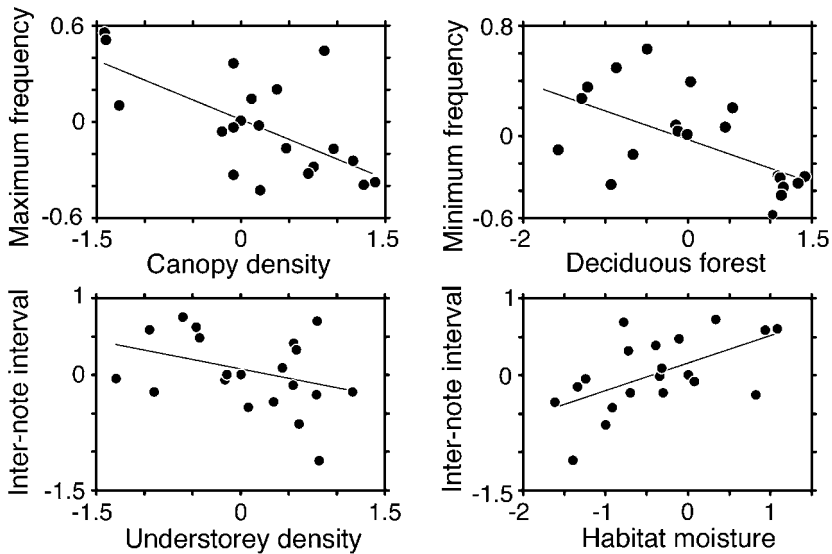


Fig. 6.12 Relations between song traits and habitat structure in the North American wood warblers. Data shown are independent contrasts, controlling for phylogeny. Each data point thus represents a single radiation in the phylogeny, with 2-13 daughter taxa per radiation. Modified after van Buskirk, J. 1997. *Proceedings of the Royal Society of London B* 264: 755-761, Fig. 1.

Much of the remaining interspecific variation in bird sounds undoubtedly results from the influence of sexual selection within species, shaping the signals that enhance both intrasexual competition and mate selection. The extent of inter- and intraspecific variability in birdsong is reminiscent of the variability in plumage ornaments and colors and strongly suggests that sexual selection is an important factor. In the following section, we briefly review some of the features of this intraspecific variation that appear to have been influenced by sexual selection.

6.2.3.3 Intraspecific variation

There is a vast literature on intraspecific variation in bird song, much of which has been recently and admirably reviewed. In the context of this chapter we cannot possibly review this subject comprehensively so we have instead chosen a few topics that we hope will give some insights into the diversity of song traits that vary within species. It is expected that much of this variation is the result of sexual selection for honest signaling. It has proven, however, very difficult to obtain clear evidence that song is costly or condition dependent enough to maintain such honesty (Gaunt *et al.* 1996), though it now seems likely that the diversity of constraints on song performance has been underappreciated (Gill and Gahr 2002; see also Song vigor, below).

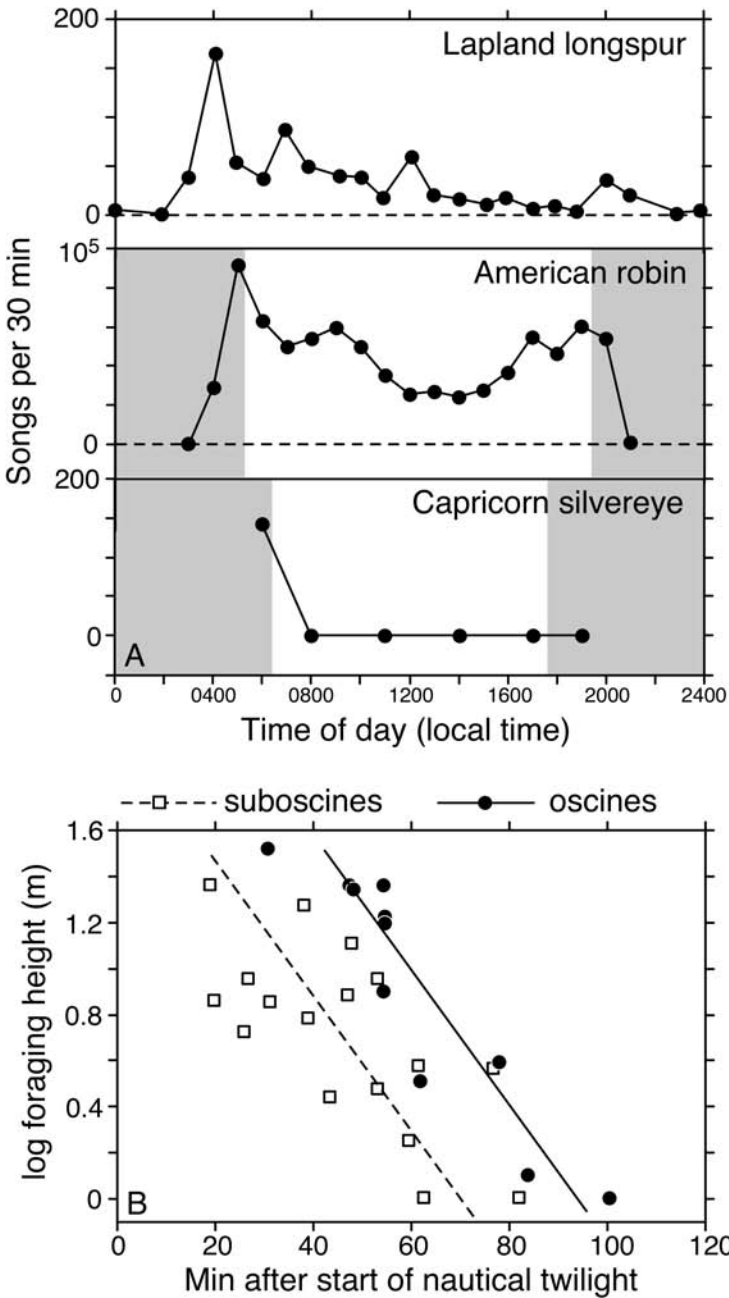


Fig. 6.13 Dawn chorus. **A.** Timing of song output in neighborhoods of Lapland longspurs breeding in high arctic Canada, American robins breeding in temperate zone Canada, and Capricorn silvereys (*Zosterops lateralis chlorocephalus*)

Song repertoires. Sexual selection might explain the intraspecific variation in song repertoires, by two different mechanisms. First, repertoire size and complexity might be an honest signal of male quality (Fig. 6.14), including age. In the Sedge warbler (*Acrocephalus schoenobaenus*), for example, males with larger and more complex repertoires bred earlier (Fig. 6.14C; Catchpole 1980), an observation nicely confirmed by playback experiments to hormone-implanted females (Catchpole *et al.* 1984). Male sedge warblers sing up to 70 different syllables types, stringing as many as 50 syllables together into a single song. Interestingly, males with larger repertoires have fewer blood parasites (Buchanan *et al.* 1999), and contribute more to parental care (Buchanan and Catchpole 2000). In the related Great reed warbler (*A. arundinaceus*), males with larger repertoires were more likely to survive to breeding age (Fig. 6.14D) and, when they did breed, cuckolding males had larger repertoires than pair males, indicating a female preference for sires with larger repertoires (Hasselquist *et al.* 1996). Because cuckolders contribute nothing to females but their sperm, genetic benefits are implicated here. In these cases, repertoire size and complexity may signal such things as current health and condition, the ability to learn and remember, and if songs are learned from neighbors, the amount of experience in the local neighborhood, as well as unknown aspects of genetic quality. A related hypothesis suggests that the early environment may have an important influence on a bird's ability to learn songs, and some evidence supports this hypothesis, too (Nowicki *et al.* 2002).

Second, when repertoires are similar (or identical) among neighboring males, experience in the local habitat might be signaled. In Lapland longspurs, repertoires appear to be learned during the first breeding season and fixed for life (R. Montgomerie unpublished data). Thus, males in a given neighborhood who sing the local repertoire (song) honestly advertise that they have experience in that habitat. Male Lapland longspurs that sing the neighborhood song have higher reproductive success than males who sing foreign songs (Mullie 1991) but whether or not females prefer local males as within and extrapair sires is unknown, although this appears to be the case in White-crowned sparrows (*Zonotrichia leucophrys oriantha*; MacDougall-Shackleton *et al.* 2002).

In a given population, both factors could also be operating, such that sexual selection could favor both repertoire size/complexity and neighborhood identity/experience. To the best of our knowledge, these two functions of repertoires have not been tested in the same species, and there is

Fig. 6.13 Contd. ...

breeding in tropical Australia. Shading indicates night. Original. **B.** Relation between the timing of the dawn chorus and foraging height above ground for 27 passerine species in an Ecuadorean rainforest. Modified after Berg, K. S. Brumfield, R. T. and Apanius, V. 2006. Proceedings of the Royal Society of London B 273: 999-1005, Fig. 2b1.

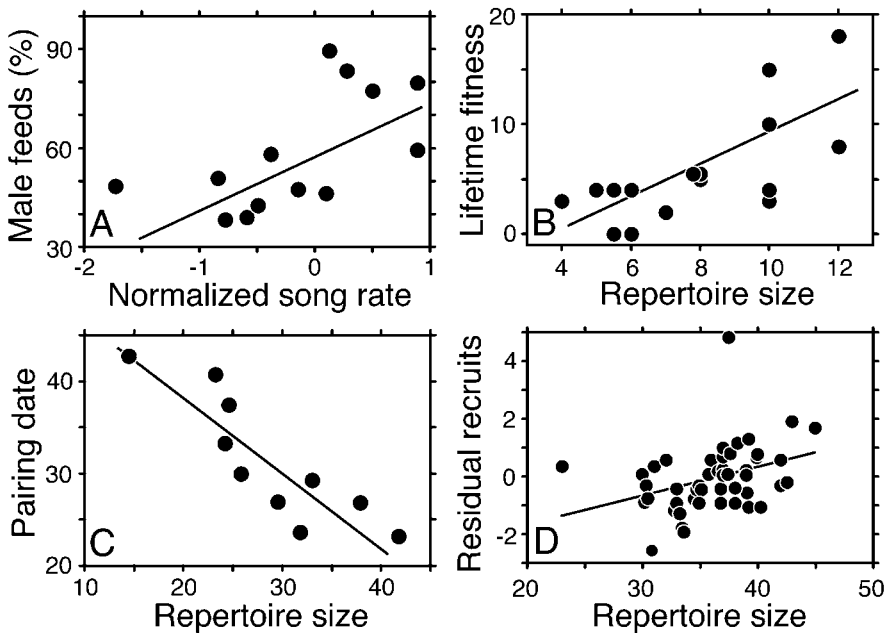


Fig. 6.14 Relations between reproductive performance and song traits in **A.** Stonechats (*Saxicola torquata*), modified after Greig-Smith, P. W. 1982. *Animal Behaviour* 30: 245-252 Fig. 6. **B.** Song sparrows (*Melospiza melodia*), modified after Searcy, W. A. 1984. *Behavioral Ecology and Sociobiology* 14: 281-286. **C.** Sedge warblers, modified after Catchpole, C. A. 1980. *Behaviour* 74: 146-166, and **D.** Great reed warblers, modified after Hasselquist, D., Bensch, S. and von Schantz, T. 1996. *Nature* 381: 229-232, Fig. 2b.

tremendous scope for further evaluation of both these hypotheses in birds. Moreover, while these examples are interesting and informative, many other studies have failed to find evidence that repertoire size influences mate acquisition or reproductive success, once confounding factors have been controlled (for reviews see Vehrencamp 2000; Marler and Slabbekoorn 2004). However, the complexity of song traits that might influence either male-male competition or female choice is so great that clear observational and experimental evidence in support of these hypotheses may simply be hard to come by even if they are generally true. In addition to the subtleties of measuring female choice, especially with respect to extrapair males, the study of repertoires remains a challenge for ornithologists interested in the influence of sexual selection on birdsong.

Song vigor. Both the loudness and duration of singing are expected to be influenced by sexual selection for honest advertisement, as neither of these traits can be bluffed by males of low quality (e.g., Vehrencamp 2000). Thus males in poor health or body condition are unlikely to be able to sing as loudly as males in good condition, and males who can sing for long periods without a break signal both that they are in good condition and that they can afford to

spend time singing instead of foraging. Thus extended singing appears to be a handicap *sensu* Zahavi (see Chapter 5). Moreover, louder and more persistent songs are more likely to attract predators and reveal the singer's location so males that deliver such songs also reveal their ability to avoid predation.

To the best of our knowledge, the signal function of song loudness has yet to be explicitly tested in birds, as song amplitude is a notoriously difficult attribute to measure in the field. Nonetheless, several studies are at least consistent with the song output/duration hypothesis. In an experimental study of Savannah sparrows (*Passerculus sandwichensis*), where some males were provided with supplemental food and other were not, food-supplemented males sang more during the dawn chorus (Reid 1987), suggesting that current body condition influences song output. Similarly, high-ranking male Black-capped chickadees (*Poecile atricapillus*) have a greater song output during the dawn chorus than low-ranking males (Otter *et al.* 1997).

Song rate and song matching. The rate at which a male sings, in relation to the songs of neighbors, and a male's ability to match the notes of a neighbor's song might also be honest advertisements of male quality in both intra- and intersexual signaling. In many species, males time their songs to closely follow the notes of a rival male and often match notes of rivals. There is a large literature on song matching and considerable evidence that this is not accidental (see Vehrencamp 2000; Gil and Gahr 2002; Marler and Slabekoon 2004 for recent reviews).

Thus in the Tufted titmouse (*Parus bicolor*), for example, males tended to match song 'themes' when countersinging with neighbors, and were more likely to engage in countersinging if they were able to match themes, in both natural singing bouts and playback experiments (Schroeder and Wiley 1983). In many species, song matching is associated with male-male aggression with either the presence or absence of matching associated with escalation. Vehrencamp (2000) has a useful discussion of the costs and potential coding rules associated with song matching.

The rate at which individuals sing and switch between different song types entails greater energy costs, and faster switching rates result in more retaliation from rivals (see Vehrencamp 2000 for review). Thus song rates have the qualities of an honest signal and are thus likely to be influenced by sexual selection. In lekking Sage grouse (*Centrocercus urophasianus*), displaying males spend at least twice as much energy per day as males that do not display (Vehrencamp *et al.* 1989), and females prefer to mate with males who have higher display rates (Gibson 1996). Similarly, in the Savannah sparrow, male song rate is positively correlated with territory quality, and females prefer to mate with males who sing at a higher rate (Reid 1987).

Dawn chorus. Most diurnally active male birds sing most often at first light during the breeding season (Fig. 6.13A). This dawn chorus remains enigmatic though a variety of hypotheses have been proposed to explain it. Given that singing enhances a male's fitness via intra- and intersexual selection,

whenever it is presented, the timing of singing may simply be influenced by natural selection for singing when it is least costly and most effective. Thus birds may sing at dawn because it is the time of day when winds and temperatures are most conducive to sound transmission enhancing the distance that sound travels and minimizing attenuation (Mace 1987). Because foraging efficiency is predicted to be low during crepuscular hours, dawn singing may be favored rather than singing during the period when foraging is most profitable (Mace 1987). There is some theoretical support for this idea, but empirical studies that address it are lacking.

Alternatively, dawn song may be a form of honest advertisement (Montgomerie 1985; Mace 1987) and thus influenced by sexual selection. This hypothesis suggests that birds sing at dawn because it is the least, rather than the most, favorable time for singing. Thus, following the 8-12 hours of dark when temperate and tropical zone diurnal birds are asleep and fasting, the quality of the dawn song might well reflect the individual's body condition resulting from the previous day's activities. Because these songs are given before any foraging is done, they are predicted to be most costly and, thus, difficult to perform, especially by low quality individuals. In both the Savannah sparrow and Lapland longspur, males with supplemented food supplies sang earlier than males without supplemental food, suggesting that the timing and vigor of songs given during the dawn chorus may reflect male condition, in accordance with this hypothesis (Reid 1987; R. M. unpublished data).

Intraspecific variation in dawn chorus timing and effort has rarely been investigated but such studies are needed to evaluate the hypotheses outlined above (but see Berg *et al.* 2006). These hypotheses are very difficult to distinguish by observations alone and critical experiments are clearly needed to determine whether the dawn chorus is simply an epiphenomenon of selection for the timing of other activities, is the result of selection to maximize signal transmission, or is under the influence of sexual selection via honest advertisement.

Duetting. Duets are joint acoustic displays where two birds sing their songs with some degree of temporal precision (Hall 2004). In some species, duets are performed by individuals of the same sex (e.g., Trainer and McDonald 1995). The most common type of avian duet, however, involves coordinated vocal displays performed by members of a mated pair (Hall 2004), but there is tremendous interspecific variation in the form of duets (Fig. 6.15). In some species, antiphonal duets are created when males and females alternately sing elements of a duet song in a highly precise and coordinated manner (e.g., Fig. 6.15B, C; Mann *et al.* 2003), whereas in others, duets consist of entire male and female songs sung alternately or in a partially overlapping manner (e.g., Fig. 6.15A, D; Mennill and Vehrencamp 2005). Alternatively, males and females sing similar song elements in synchrony (e.g., Wickler and Seibt 1980) to create a polyphonal duet. Coordinated visual displays (see Courtship Displays) and group choruses (Baker 2004; Mann *et al.* 2006) may serve analogous functions in some situations.

Duetting is taxonomically widespread, occurring in a number of distantly related species, and is therefore thought to have evolved independently several times (Farabaugh 1982; Hall 2004). Nevertheless, duetting is relatively uncommon, having been reported in fewer than 3% of species (Farabaugh 1982), although this is almost certainly an underestimate (Hall 2004). Duetting appears to be more common in birds with tropical distributions (Thorpe 1972; Farabaugh 1982; Langmore 1998).

Avian duets have long been of interest to naturalists, and early studies and observations focused on the duetting pair as a unit, considering duets in a similar context to male solo songs and interpreting duetting as a cooperative behavior (Hall 2004). Only recently has duetting been investigated in an evolutionary context, including the possibility that duetting may actually represent a source of conflict between the sexes (Levin 1996; Langmore 1998; Hall 2004). Several hypotheses have been proposed to explain the adaptive significance of avian vocal duets, and these have recently been reviewed in detail by Hall (2004) who categorizes these hypotheses according to whether they are primary or secondary explanations for duetting behavior, the intended signal receiver, the information being conveyed, and whether the hypothesis represents a potential source of conflict between mated partners. Briefly, these hypotheses are: maintaining contact with partner, ensuring reproductive synchrony, mate guarding, paternity guarding, preventing a partner being usurped, joint resource defense, signaling quality, signaling commitment, sex recognition, maintaining reproductive isolation, ritualized appeasement, and protection from predators (Hall 2004). Thus, duetting may serve a variety of functions, including both courtship and territory defense. Much more work is needed, however, to assess the relative importance of each of these hypotheses. More than likely, the function of duets differs between species, and multiple functions may co-exist within species. Recent methodological advances including molecular genetic sexing (Griffiths *et al.* 1998), stereo-duet playback techniques (Rogers *et al.* 2004; Mennill 2006), and acoustic location systems (Mennill *et al.* 2006) are likely to enhance our understanding of the adaptive significance of duetting. Comparative analyses of the ecological and social correlates of duetting, which are currently lacking, provide another promising avenue for future research.

Vocal mimicry. Most birds that learn their songs probably copy some notes from neighbors and parents during the process of song acquisition. A few species, though, copy sounds from their environment and, in some, these copied sounds form a major component of their vocal repertoire. Sounds copied from conspecifics are usually classified as imitation whereas those from the environment are examples of mimicry. In some cases the mimicked sounds appear to have a foraging or antipredator function but in others, the function is clearly mate attraction or intrasexual interaction (Baylis 1982).

Vocal mimicry is a widespread phenomenon in birds, having been recorded in about 15% of passerines in Australia, Britain, and South Africa (Baylis

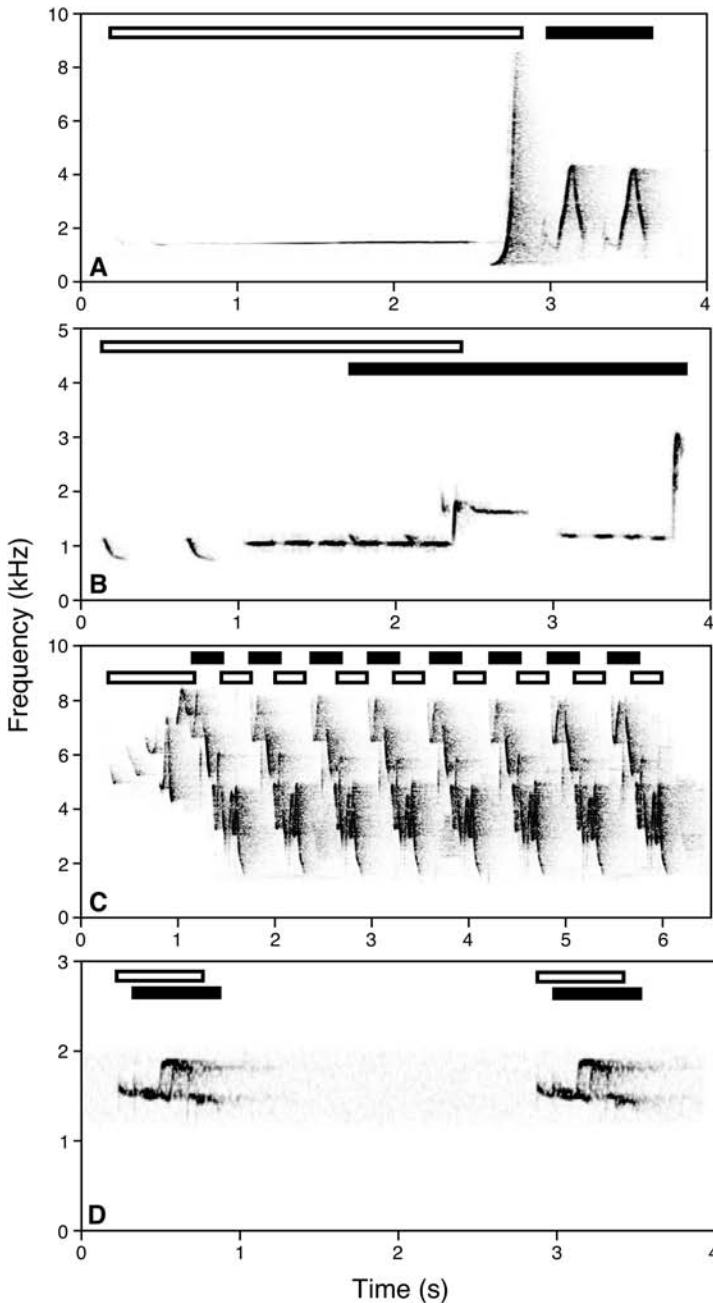


Fig. 6.15 Some examples of different types of avian duets. Each sonogram shows two individuals (identified by black and white bars above their respective syllables) coordinating their vocalizations and thus producing duets. **A.** Antiphonal duet of the

1982), and a wide variety of bird families. Some families (Menuridae, Sturnidae, Mimidae) have a high proportion of species that are mimics, and mimicry has so far only been documented in the suborder Passeri (oscines) suggesting at least some phylogenetic influence on this behavior. Predominance in the Passeri is not so surprising because this taxon is distinguished by both a complex voice box (syrinx) and song learning. Mimicry also appears to be relatively rare in migratory species and more common in larger songbirds (Hartshorne 1973) for reasons that are not clear and deserve further study. There is no obvious relation between vocal mimicry and habitat or mating system, and some instances of apparent mimicry are undoubtedly accidental, serving no adaptive function (Baylis 1982).

The lyrebirds (family Menuridae) of Australia are probably the most accomplished mimics, producing songs virtually indistinguishable to the human ear from those of many other bird species that sing in their neighborhood (Fig 6.16), as well as insects, wingbeats, chain saws, camera shutters, and other ambient noises. Robinson and Curtis (1996) could find no evidence that lyrebirds mimicked anthropogenic sounds, but David Attenborough's 'Life of Birds' clearly showed a male Superb lyrebird (*Menura novaehollandiae*) make the sound of a camera shutter followed by the electronic winding of the film, among other excellent renditions of ambient sounds. The Marsh warbler (*Acrocephalus palustris*) of Europe is also an accomplished mimic, with up to 80% of a male's large repertoire during the breeding season comprised of notes copied from other species, including many that breed on this warbler's winter range in Africa (Baylis 1982). The brood-parasitic indigobirds (family Viduidae) of Africa are also accomplished mimics, precisely copying the songs of their hosts (Payne 1982).

Because vocal mimicry results in larger song repertoires, it seems likely that the same hypotheses proposed to explain the advantages of larger repertoires would apply (see above), when the mimicked songs are used in inter- and intrasexual interactions during the breeding season. These explanations do not apply, however, to the vocal mimicry of the nineteen species of parasitic indigobirds (genus *Vidua*). In those birds, males mimic the songs of their brood parasitic hosts, which they learn as nestlings in the foster parent's nest (Payne and Payne 1995). In the indigobirds, the vocal mimicry signals to females information about the genetic lineage of the male, as different lineages

Fig. 6.15 Contd. ...

Eastern whipbird (*Psophodes olivaceous*) showing a male (white) introductory whistle and whipcrack followed by the female's (black) 'chew-chew' response. **B.** Antiphonal duet of the Rufous-and-white wren showing a male (white) song partially overlapped by a female (black) song. **C.** Antiphonal duet of the Plain wren (*Thryothorus modestus*) showing a male (white) introductory phrase followed by alternating female (black) and male phrases. **D.** Polyphonal duet of the Long-tailed manakin (*Chiroxiphia linearis*) showing an alpha (white) and a beta (black) male singing their 'toledo' vocalizations in unison. Original recordings and sonograms by D. J. Mennill.

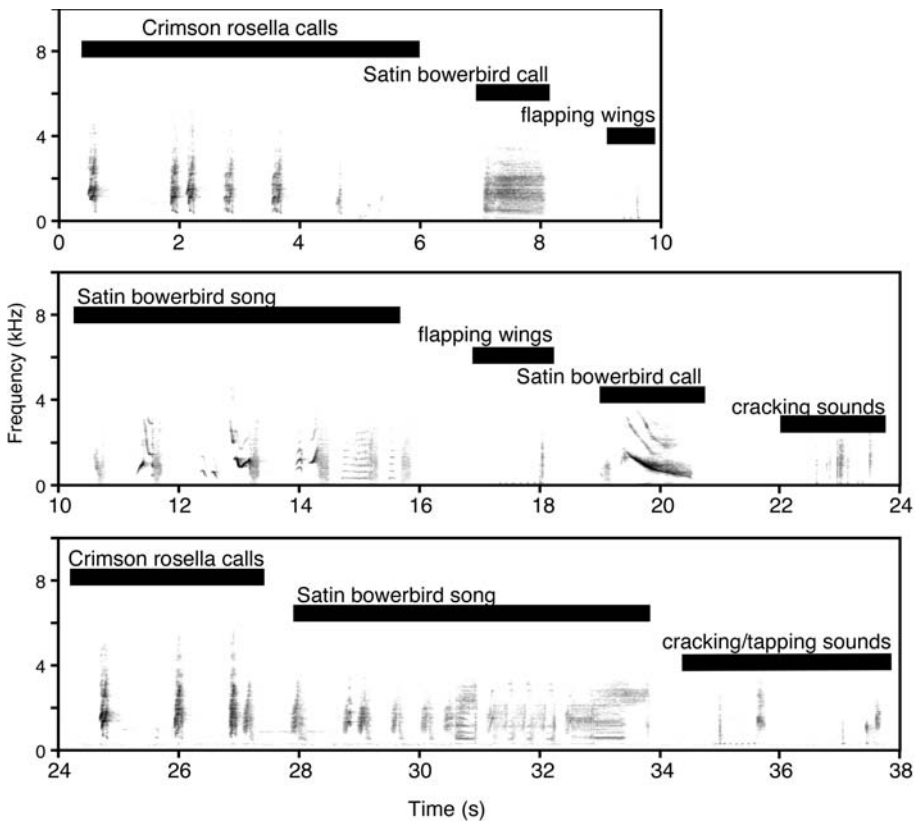


Fig. 6.16 An example of vocal mimicry in the Albert's lyrebird (*Menura alberti*). Species and sounds mimicked are indicated on the sonogram. All sounds are made by the bird's syrinx, including wing sounds. Original sonogram by R. Montgomerie from a recording by Sydney Curtis, who also identified the mimicked sounds.

seem to be adapted to different hosts (also mimicking the mouth lining patterns of the hosts nestlings, and possibly other traits). Thus by choosing a mate who sings the same songs as her own foster parents, a female ensures that her offspring will be able to survive in the host's nest.

Vocal mimicry in the Marsh warbler may also signal something useful to females about the life history of potential mates. Since many of the songs that males mimic in this species are learned on the wintering grounds, these songs are honest indicators of the male's winter range and migratory route and this may be important to females if there is an advantage to assortative mating with respect to this trait (Baylis 1982). In the closely related Black-browed reed warbler (*A. bistrigiceps*), however, there was no clear evidence that females preferred males with larger mimetic repertoires (Hamao and Eda-Fujiwara 2004). In that study, though, sample sizes were small ($n = 18$) and effect sizes relatively large, suggesting that a significant relation might be revealed with a larger sample.

The large vocal repertoires of Northern mockingbirds (*Mimus polyglottos*) in North America are composed of both mockingbird-specific songs and the songs of other species in their breeding neighborhoods. Derrickson (1988) found that song versatility, a measure of the diversity of song types used, peaked during the courtship phase. Males that had the highest song versatility tended to be the first to acquire mates and begin nesting (Derrickson 1988), suggesting that females prefer males with more versatile songs. While these results are intriguing in the context of sexual selection, some experimental work is needed to confirm a cause and effect relation here.

Despite decades of interest in vocal mimicry in birds we are still a long way from understanding the factors that influence its occurrence, except in the parasitic indigobirds (Payne 1982). Since mimicry increases repertoire size, it seems likely that hypotheses to explain the evolution of repertoire size are likely to apply, with the added complication that the sounds mimicked are an important component of the variation among individuals. The technical tools are now available to make a detailed experimental study of vocal mimicry feasible in birds.

6.2.4 Courtship Displays

Most birds perform behavioral displays during courtship, usually employing the various types of ornaments and some of the sounds described above. Although most species perform courtship displays on the ground and/or in vegetation (e.g., Figs. 6.3A,F, 6.4C, 6.5C, 6.6A,E, 6.7A,C and 6.8B,C,E-G), some of the most visible and spectacular displays occur in the air or on the water (Figs. 6.3G, 6.7B,D and 6.8A,D). Aerial displays are most common among species that breed in open habitats (e.g., waders, larks, pipits; Figs. 6.7D and 6.8D) where they perform stereotyped song flights, as well as in those species known for their flight agility, such as swifts, swallows, hummingbirds, nightjars (Figs. 6.3E,G and 6.7B), and birds of prey. Because aerial displays place particular demands on morphology, evidence is growing that sexual selection for flight agility favors smaller relative body size in males (Hedenström and Møller 1992). Waterfowl, loons and grebes all display on the water, with the synchronized dances of grebes being among the best studied (e.g., Huxley 1914) and least understood courtship behaviors in birds.

6.2.5 Why Birds Court

Why do birds court? There is no simple answer to this question, as there may be many different functional explanations for the evolution of courtship in birds. Moreover, these different explanations need not be mutually exclusive, and may operate simultaneously to shape a species-typical courtship behavior. This diversity of functional explanations for courtship had either gone unnoticed or was overlooked in favor of a particular hypothesis in many early reviews of this topic. Moreover, progress towards understanding the diversity of functions of courtship may have been hindered by the tendency of some authors to anthropomorphize. Early writers, in particular, all too often

ascribed particular meaning to courtship rituals involving a male presenting flowers to a female, a mated pair performing an elaborate and coordinated dance, or a pair of birds engaging in frequent copulations.

Clearly, there is extensive variation in the degree of elaboration of courtship behavior among bird species. A large number of hypotheses has been proposed to explain the adaptive significance of courtship in birds, but these are scattered among both the primary and secondary literature, and have not, to the best of our knowledge, been summarized in a single review. While we are certain that the list of hypotheses we evaluate in this section is not exhaustive, we have tried to review most of the major hypotheses (Table 6.2). We present each of these in a form that is consistent with current ideas about the action of natural and sexual selection, rather than necessarily in their original form, as this would sometimes make little sense in a modern context. We then discuss the context under which each mechanism is likely to be influential, and provide an example of supporting evidence whenever possible.

H1 Courtship is not functional

As a null hypothesis, it is important to consider the possibility that some courtship behavior may not serve any current adaptive function. Thus some forms of courtship or specific displays may have originally evolved for a particular purpose but currently serve no function, existing merely as remnants of some past adaptive value or even resulting from a correlated response to selection on other traits.

Context. Some early authors suggested that the elaborate pair displays used well past the breeding season by albatrosses and gannets are performed out of habit or as a form of play, and have no particular adaptive significance (e.g., Townsend 1920). Alternatively, some courtship may have evolved simply via genetic drift, or may be expressed as a byproduct of some other functional behavior or physiology. As reviewed by Townsend (1920), it was long believed that male courtship displays were merely reflex actions resulting from excessive excitement and that these had no effect whatsoever on females.

Table 6.2 Summary of major hypotheses explaining the function of courtship in birds

H1	Courtship is not functional (null hypothesis)
H2	Coordinate/stimulate physiologies
H3	Maintain the pair bond
H4	Gain information about mate/coordinate breeding activities
H5	Enhance mate condition
H6	Facilitate species recognition
H7	Facilitate sex recognition
H8	Mate attraction...
	H8.1 ...using indicator traits
	H8.2 ...using sexy traits
	H8.3 ...using sensory exploitation
H9	Mate guarding
H10	Manipulate the mating partner

Supporting evidence. There is limited evidence from experimental studies of Japanese quail (*Coturnix japonica*), in captivity, that the absence of certain elements of male displays may not influence a female's willingness to copulate (Wilson and Bermant 1972). That does not, of course, mean that these elements do not influence the females' mating decisions as there are certainly opportunities for the female to bias paternity after copulation (Chapters 7, 8).

Future directions. Probably the best prospect for studying the influence of particular courtship traits on mating decisions comes from controlled experimental studies in the laboratory using videotaped or animated stimuli (e.g., Turnell *et al.* 2003). In such studies, individual courtship traits (plumages, songs, displays) can be omitted from the courtship sequence to examine their effects on mate responses, and, particularly, paternity.

H2 Coordinate/stimulate physiologies

Courtship displays performed by either sex may serve as a form of advertisement of readiness and/or willingness to breed, or may even stimulate a potential partner to enter into breeding condition. There were many early proponents of this idea (e.g., Huxley 1914; 1923; Stonor 1940; Armstrong 1947). For example, Stonor (1940) wrote that "...when a Goldeneye Drake throws his head daintily into the air, or shoots it out on the water...the females are seeing something quite out of the ordinary, that they do not see at other times of the year, and something that by its very strangeness both attracts them to the male responsible and keys them up...so that they are stimulated to begin and carry out the breeding cycle which the courtship ushers in". Stonor (1940) also suggested that the displaying male is likely to become as stimulated by his own display as the female he is displaying to. Huxley (1923) relied heavily on this explanation, whereby courtship serves as a naturally-selected regulator of breeding physiology, to build his argument against Darwin's theory of sexual selection.

Context. Although research on mating signals has recently made tremendous progress in the context of sexual selection (Andersson 1994; Ligon 1999), some of the functions suggested by early behaviorists may not have been too far off the mark. The seasonal activities of birds (e.g., molt, migration, breeding) are triggered proximately by endocrine changes (Volume 6A, Chapter 5). These changes are mediated by an endogenous circannual rhythmicity that is kept in check by predictable environmental cues, such as changes in photoperiod that trigger gonadal development in many species (Gwinner 2003; Volume 6A, Chapter 5). Endocrine changes are then fine-tuned by other environmental cues, such as changes in food availability and the interaction with conspecifics (Hinde 1965), and it is at this stage that courtship can play a stimulatory role.

Courtship may thus play a particularly important role in the stimulation of breeding behavior or the coordination of breeding efforts between partners when environmental cues are unreliable or absent (Kunkel 1974; Hall 2004), as they often are in the tropics. Other cues may be available, such as seasonal

changes in light intensity at the onset of a rainy season (Gwinner 2003), but they may not be as predictable or reliable as changes in photoperiod and thus may serve as only rough indicators for breeding that need to be finely-tuned by mated pairs. Also, in many socially monogamous species, courtship rituals continue to take place well after pairing, when there is no obvious mating decision to be made (Huxley 1914; Wachtmeister 2001). In this situation, courtship may enhance reproductive synchrony.

Supporting evidence. Despite its long standing as the favored hypothesis for explaining the function of courtship in birds, there were surprisingly few early attempts to rigorously test this idea. Nevertheless, there has been a recent surge of research on this topic, with several studies supporting the stimulatory role of courtship behavior, with particular focus on the interaction between endocrine-based reproductive physiology and courtship (Cheng 1993). Beginning with the work of Hinde (1965), experiments on captive Canaries (*Serinus canaria*) and Ring doves (*Streptopelia risoria*) have been especially informative in this respect.

Further evidence in support of this hypothesis comes from both experimental and observational studies that were actually focused on other questions. Female canaries, for example, built their nests faster and laid more eggs when exposed to larger male song repertoires (Kroodsma 1976), and in the Ring Dove, the coos delivered by females in response to male display trigger an endocrine response that stimulates their own ovulation (Cheng 1993). Similarly, the role of courtship in coordinating physiologies has been frequently invoked to explain the function of vocal duets (Hall 2004).

Future directions. Some difficulties associated with designing appropriate experiments to test the stimulatory role of courtship are highlighted by the studies mentioned above. In some species, the mere presence of a potential breeding partner may have a stimulatory effect, irrespective of the courtship signal. For example, in mate choice experiments using song playback, broadcast song is the only available cue of male presence, so females may simply be responding to the perceived presence of a potential breeding partner. Also, some of the anecdotal evidence described above originates from mate choice experiments designed to test female preference for variation in male traits, so a female's response to the stimulatory effects of courtship display must be separated from her response to, or preference for, certain sexual ornaments.

H3 Maintain the pair bond

One of the earliest explanations for the courtship behavior of birds is that it serves to maintain the pair bond, though the meaning of the term 'pair bond' is never really made clear.

Context. Notwithstanding the difficulty in defining the pair bond, this hypothesis requires that courtship *per se* results in a pair staying together in the absence of any other reason for maintaining the partnership.

Supporting evidence. The problem with this hypothesis is that the pair bond is a nebulous concept. Thus what has been called a pair bond may simply be a manifestation of mate guarding (see H9; Montgomerie 1986), the coordination of partner activities and physiologies (see H2), or the association that results from copulation, nest-building and biparental care. To the best of our knowledge, there is little convincing evidence that pair associations (bonds) in birds are maintained because of some psychological bond that transcends and persists when there are better options for maximizing fitness. Evidence for the lifetime pair associations in several species (e.g., swans, fulmars) could potentially be interpreted in support of this hypothesis, and there are certainly many anecdotal observations to suggest that some birds form an emotional bond to their mate.

Future directions. To support this hypothesis it is necessary to show that individuals perform courtship displays to show their willingness to engage in reproductive activities, and that the signal receivers decide to remain paired as a result of those signals even when better options are available.

H4 Gain information about mate/coordinate breeding activities

One potential function of courtship is that it informs the receiver about the signaller's strengths and weaknesses, and breeding readiness (e.g., Cézilly *et al.* 2000). Such a function may be favored via several different mechanisms. For example, learning about a mate's weaknesses may allow individuals to adjust their own behavior to compensate, particularly with respect to parental care. Alternatively, certain types of courtship signals may have evolved as a result of selection to facilitate the coordination of breeding activities in which both pair members participate, such as nest-building or feeding offspring. Learning about one's mate through courtship may also serve as a form of continuous assessment of mate quality. This latter function is a component of the mate attraction hypotheses (H8) described below.

Context. Courtship that allows birds to learn about each other may be favored by either natural (compensation, signaling intention) or sexual selection (continuous assessment), and may depend somewhat on the mating system. Thus, the use of information gained in courtship to compensate for a partner's shortcomings, or to coordinate breeding activities, should be more common in socially monogamous species where both pair members contribute to rearing the offspring. By contrast, continuous mate assessment may be favored in species where serial monogamy, divorce, or extrapair copulations are known to occur (Cézilly *et al.* 2000).

Supporting evidence. To our knowledge, the hypothesis that avian courtship provides information that enables an individual to adjust its own behavior for the benefit of the pair has not been systematically tested, though some anecdotal observations are consistent with this hypothesis. For example, in many birds with biparental care, one sex will usually compensate for low nestling-feeding rates by their partner (e.g., Jones *et al.* 2002). It is not known, however,

whether birds use courtship cues to evaluate their mate's potential contribution to parental care rather than assessing parental investment directly.

Future directions. The paucity of studies on courtship as a procedure for learning about one's mate makes this a promising avenue for future research. There are obvious logistic challenges to testing this hypothesis experimentally, and future tests may need to rely on observational and comparative studies.

H5 Enhance mate condition

In many species, male birds provide food to females during courtship (Lack 1940) and a number of hypotheses have been proposed to explain the function of such courtship feeding. In some cases, males obtain pair or extrapair copulations as a result of courtship feeding (e.g., Mougeot *et al.* 2002; Helfenstein *et al.* 2003). Such a function would fall under the mate attraction hypotheses described below (H8), and will not be discussed here. Instead, we are concerned here with the hypothesis that courtship feeding enhances female condition and, presumably, pair reproductive success. This hypothesis has occasionally been called the nutritional hypothesis.

Context. Courtship feeding in general should be more common in socially monogamous species that share parental duties and particularly in species where the female expends considerable energy during egg production and incubation.

Supporting evidence. Several studies support the hypothesis that courtship feeding enhances female condition. In Amazon kingfishers (*Chloroceryle amazona*), for example, the incidence of male courtship feeding influenced the likelihood that females would lay eggs and also the egg-laying date (Davis and Graham 1991). Some studies also suggest that, by feeding their mates, males enhance pair reproductive success (e.g., Helfenstein *et al.* 2003), although it often remains unclear whether this enhanced success is a direct consequence of improved female condition, or whether it is the result of differential allocation by females when they are mated to high-quality partners (e.g., Burley 1988).

Future directions. Courtship feeding appears to serve different function in different species (Lack 1940; Smith 1980), and different functional hypotheses for the evolution of courtship feeding, including sexual selection hypotheses, should be tested in concert. Surprisingly, we found no published comparative analyses testing this hypothesis, even though comparisons among closely related species appear to be quite telling (Smith 1980). Because of potential confounding variables, intraspecific tests of the nutritional hypothesis are strengthened by experimental food supplementation, and future studies should target this approach.

H6 Facilitate species recognition

One of the earliest ideas about the courtship behavior of birds is that songs, displays and colors are adaptive because they facilitate species recognition

(see Mayr 1963) and thus minimize the costs of unwanted interspecific pairing (mainly infertility).

Context. This idea is related to the general concept of species' isolating/recognition mechanisms, wherein traits are thought to evolve to be different in closely related species via selection that reduces or eliminates mating errors that might accrue from failing to distinguish conspecifics from similar-looking individuals. The fact that some closely-related species differ in their courtship behaviors was thought to be important in this context whenever their ranges overlapped (Mayr 1963).

Supporting evidence. Much evidence has been presented in support of the species recognition hypothesis but not much of it provides clear support exclusive of the other hypotheses that we describe (Table 6.2). For example, the fact that a female does not respond to a male with altered display traits may signify only that she perceives that male as being of low quality (see H8.1). Interestingly, the birds of paradise, which have some of the most elaborate courtship displays known in birds, have one of the highest rates of intergeneric hybridization in the wild (Frith and Beehler 1998). Thus, at least in that family, elaborate courtship does not appear to facilitate species recognition.

Probably the best evidence in support of this hypothesis comes from research on apparent reproductive character displacement between Collared (*Ficedula albicollis*) and Pied flycatchers (*F. hypoleuca*) in regions of sympatry in central and eastern Europe (Saetre *et al.* 1997). In these species, it seems that male plumage colors have diverged in sympatry as a result of female choice and, consequently, the incidence of hybridization is reduced (Saetre *et al.* 1997). Whether or not courtship behavior as well as plumage colors have diverged in sympatry is unknown but certainly warrants further study.

Future directions. The biggest challenge in testing this hypothesis will be to control for confounding variables linked to other hypotheses that explain why birds court. Some progress might be made by seeking out other potential examples of reproductive character displacement like that in the *Ficedula* flycatchers, especially with respect to displays. It seems to us, however, that species recognition is most likely to be a factor shaping courtship in the early stages of speciation and much less important than the other forms of selection on courtship displays in shaping the eventual suite of traits that birds use to influence potential mates.

H7 Facilitate sex recognition

Another early hypothesis for the function of ornaments and behaviors used in courtship is that they help facilitate sex recognition.

Context. Sex-specific behaviors and vocalizations may be particularly important in species that are sexually monomorphic, whereas sexual dimorphism might facilitate the rapid visual identification of members of the

opposite sex, thus saving time and energy, and potentially reducing injury from aggressive responses.

Supporting evidence. It is clear that many birds use a variety of existing, sex-specific traits to identify members of the opposite sex (e.g., Nuechterlein and Buitron 1992; Saetre 1993). It is less clear, however, whether these traits originally evolve to facilitate discrimination, or whether they are simply co-opted for this function once they have evolved and become reliable indicators of sex. Moreover, many courtship ornaments and displays appear to have been elaborated to a level far beyond what should be necessary for sex recognition.

Future directions. Courtship traits may facilitate sex recognition but, in many species, do not appear to be absolutely necessary for this task. Thus it seems unlikely to us that many traits will be found to function only to signal sexual identity.

H8 Mate attraction

Darwin (1871) first proposed that elaborate sexual ornaments, like many of the traits used in courtship, could evolve by sexual selection via female mate choice or male-male competition. According to the theory of sexual selection, elaborate ornaments can evolve if heritable variation in these traits enables some individuals to outcompete others for mates (Andersson 1994). Three related hypotheses, described below, postulate that courtship serves a mate attraction function and thus has evolved via sexual selection. While all of these are mate attraction hypotheses, they differ in the types of signals used when attracting mates and the consequences for potential mates responding to these signals. For all three hypotheses, we assume that a mate attraction function can extend beyond the current partnership to include attracting extrapair copulations or securing future mating opportunities.

H8.1 Mate attraction using indicator traits

The indicator or handicap hypothesis proposes that elaborate courtship signals are attractive to members of the opposite sex because they honestly reflect the quality of the bearer. According to Zahavi's handicap model (Zahavi 1975; Chapter 5), costly ornaments reveal quality because only high-quality individuals can bear the costs of these traits (Kodric-Brown and Brown 1984). According to indicator models, females stand to gain either direct material benefits or indirect genetic benefits by basing their mate choices on such quality-indicating courtship signals.

Context. As with other sexual selection hypotheses, the evolution of sexually selected indicator traits should directly relate to the opportunity for sexual selection. Thus, indicator traits should be more likely to evolve in species with female-biased parental care and considerable variation in male mating success.

Supporting evidence. There is widespread empirical support for the hypothesis that traits used in courtship serve as quality indicators (reviewed in Andersson 1994). When the benefits are direct, the most conclusive studies

are those in which females choose males based on plumage coloration, particularly carotenoid-based colors (Chapter 2). This sort of indicator is probably favored by selection because there is a direct link between carotenoid pigments, which must be obtained from the diet, and the amount of food delivered to the incubating female or to the offspring. Such food delivery is one of the most common direct benefits provided by male birds. (Chapter 2).

Indirect, good genes benefits to mate choice are more difficult to observe and quantify, and fewer studies have been able to provide conclusive evidence for these (Andersson 1994). Nonetheless, Marshall *et al.* (2003) found that, in Sedge warblers (*Acrocephalus schoenobaenus*), male song complexity is strongly correlated with individual genetic diversity, and is a trait preferred by females. Thus, by choosing males who sing more complex songs, females may optimize genetic diversity in their offspring (Marshall *et al.* 2003), and this genetic diversity presumably enhances mean offspring viability. Similarly, Forstmeier *et al.* (2002) discovered that, in Dusky warblers (*Phylloscopus fuscatus*), males who sang louder songs gained more extrapair copulations and lived longer. Thus, by choosing those males as extrapair sires, females may have enhanced the longevity of their offspring (Forstmeier *et al.* 2002).

Future directions. Both theoretical and empirical studies support this hypothesis. However, conclusive evidence for good genes benefits remains restricted to a few species, and more research in this area is clearly warranted. With the development of increasingly sophisticated molecular tools, we are now potentially able to directly identify genes and genotypes responsible both for producing ornamental traits and for conferring viability benefits. These new techniques should greatly enhance our ability to investigate good genes models of sexual selection.

H8.2 Mate attraction using sexy traits

In his runaway model of sexual selection, Fisher (1930) proposed that female preference and the elaboration of male courtship traits could become genetically correlated and thereby rapidly coevolve. In such a scenario, females exhibiting the preference for elaborate male ornaments would produce choosy daughters and sexy sons, and this should drive the evolution of increasingly strong female preferences and elaborate male traits even in the absence of good genes and good parent benefits (Fisher 1930).

Context. As with the other sexual selection hypotheses (H8.1 and H8.3), the logic of the runaway selection hypothesis depends on the opportunity for sexual selection, which is in turn influenced by variation in female choosiness and male mating success. But, unlike the good genes hypothesis (H8.1), the genetic benefits of the runaway selection hypothesis are restricted to the production of sexy sons who will presumably experience high reproductive success.

Supporting evidence. Although the evolution of elaborate courtship signals through runaway selection has received widespread theoretical support, conclusive empirical evidence for this hypothesis is difficult to establish for

two reasons. First, runaway selection can co-occur with good genes sexual selection, making it difficult and perhaps counterproductive (Kokko *et al.* 2002) to distinguish between the two. Second, simply showing that a preferred trait is not associated with a particular material or good genes benefit is not sufficient evidence to support runaway selection, as it is difficult to quantify all of the potential benefits in any particular study. Despite this, in a phylogenetic analysis of display ornaments and behaviors in manakins, Prum (1997) discovered that morphological and behavioral novelties were independently hierarchically distributed. Based on *a priori* predictions for a variety of selection mechanisms, Prum (1997) interpreted this trait distribution as being most consistent with Fisherian and sensory bias mechanisms, rather than indicator models.

Future directions. Fisher's (1930) theory of runaway sexual selection is often implied when tests of other hypotheses produce negative or inconclusive results. However, conclusive tests of the Fisherian process are notoriously difficult to carry out. Kokko *et al.* (2002) argue that the evolutionary outcome will remain consistent whether the enhanced reproductive value of offspring stems from their enhanced attractiveness, their increased viability, or both. Nevertheless, recent theoretical models suggest that good genes and Fisherian selection likely originate from distinct inheritance patterns (Kirkpatrick and Hall 2004). For example, in birds, Fisherian sexual selection is more likely to evolve when female preferences are Z-linked, whereas good genes sexual selection is more likely when preferences are X-linked or autosomal (Kirkpatrick and Hall 2004).

H8.3 Mate attraction using sensory exploitation

Sensory exploitation models propose that courtship displays and ornaments attract mates by exploiting biases in the female's sensory system, either via sensory bias or sensory drive. Thus, the sensory bias hypothesis proposes that male ornaments exploit female preferences for particular signals that evolved in a context outside of mating (e.g., Andersson 1994; Endler and Basolo 1998). As a hypothetical example, females may develop a preference for red plumage coloration in males because of a pre-existing preference for red food items. By contrast, the sensory drive hypothesis proposes that habitat-induced differences in the transmissibility of different signals will favor courtship signals that maximize transmission efficiency in a particular habitat (e.g., Kokko *et al.* 2003). As a hypothetical example, females of a species inhabiting a forested habitat may prefer male songs with little or no rapid frequency modulation because these songs suffer less degradation in dense vegetation.

Context. Sensory exploitation models of sexual selection may be favored in a broad diversity of scenarios, and this mechanism is likely to act in concert with the other mechanisms discussed in this section. For example, sensory bias may be responsible for the origin of a particular female preference, but this may then coevolve with the male trait under runaway selection. Similarly, a pre-existing bias for red coloration in males may be reinforced by indicator mechanisms if red coloration is condition-dependent.

Supporting evidence. There is widespread empirical support for the sensory drive hypothesis in birds, particularly in relation to plumage coloration and song. For example, male birds modify the location and timing of their courtship displays to enhance plumage conspicuousness (e.g., Endler and Théry 1996), and the evolution of male plumage coloration appears to be influenced by habitat characteristics (e.g., McNaught and Owens 2002; Doucet *et al.* 2006; Hill and McGraw 2006). Furthermore, Madden and Tanner (2003) showed that, in two species of bowerbird, female preferences for food items of certain colors matched male preferences for the use of those same food items as bower decorations. The sensory drive hypothesis has also received strong empirical support in vocal communication studies, where the hypothesis has also been termed ‘acoustic adaptation hypothesis’, ‘environment adaptation hypothesis’ or ‘ecological adaptation hypothesis’. Several studies have documented associations between song characteristics and habitat, both within and among bird species (e.g., Morton 1975; Seddon 2005).

Future directions. Whereas the sensory drive hypothesis has received substantial empirical support in other contexts, evidence for the role of sensory bias in courtship displays is still relatively sparse in birds. Thus, much of the research on sensory exploitation has focused on vocal and plumage traits but it would be interesting to test these hypotheses in other courtship modalities, such as odors and behavioral displays.

H9 Mate guarding

In some situations, male courtship behavior might be adaptive because it signals to potential suitors that the female is mated and thus not available.

Context. Displays that are visible or audible to males other than the pair male might well enhance male reproductive success by signaling to those other males that the female is being guarded and is thus not worth pursuing as a potential mate. This sort of signal could be enhanced if the female actively displays or sings during courtship as well, thereby indicating that she is unavailable to other males.

Supporting evidence. Three very different kinds of courtship behavior are consistent with this hypothesis. First, this hypothesis may well explain the protracted period of courtship and copulation seen in some species (see Copulation below), beginning long before the interval when the female is fertilizable and continuing long after the pair has already formed a partnership. In the Lesser kestrel (*Falco naumanni*), for example, courtship and copulation occur daily whenever the pair arrives back at the colony site up to 2 months before egg-laying begins (Negro *et al.* 1992).

Second, the vocal duetting behavior of many tropical birds may be favored by selection because of its mate guarding function. In the Rufous-and-white wren (*Thryothorus rufalbus*), for example, mated pairs often duet when they are out of sight of one another in dense vegetation (Hall 2004; Mennill and Vehrencamp 2005).

Finally, this hypothesis may explain the extended and mutual courtship behavior of colonial seabirds, like boobies, penguins, and auks, which all court mutually and extensively at the nest site long before the egg-laying period. The close proximity of neighbors and the mutual signaling between the sexes may signal that the pair has formed a partnership, thereby discouraging the sexual advances of extrapair males.

Future directions. This mechanism may act in concert with one or more other mechanisms in shaping courtship behavior, thus making it difficult to test independently. Nonetheless, it would be interesting to experimentally interfere with mutual courtship, in particular, to test whether this changes the response of nearby males in a way that would suggest that they do not perceive the pair female as being guarded.

H10 Manipulate the mating partner

Recently, Wachtmeister and Enquist (2000) and Wachtmeister (2001) proposed that pair displays in monogamous species might become increasingly ritualized and elaborate as the result of an evolutionary arms race between the sexes. This hypothesis suggests that each sex is open to manipulation because partners should be sensitive to each other's actions. If an exaggerated, manipulative signal elicits a response that is beyond the optimal level for the receiver, the receiver should counteradapt by becoming less sensitive to the exaggerated signal. Over time, a highly elaborate signal is necessary to elicit any response at all, and thus to ensure copulation and reproduction (Wachtmeister 2001). It should be noted that this manipulation hypothesis shares similarities with the chase-away version of Fisher's (1930) runaway selection hypothesis, which suggests that females become increasingly resistant to male ornaments and that male ornaments must therefore become increasingly elaborate to overcome this resistance (Holland and Rice 1998).

Context. One strength of this hypothesis is that it can potentially explain almost any type of courtship behavior. Wachtmeister (2001) draws particular attention to the fact that, unlike some of the hypotheses described above, the courtship-as-manipulation hypothesis can explain the evolution and maintenance of post-pairing courtship displays in genetically monogamous species.

Supporting evidence. Wachtmeister and Enquist (2000) used a recurrent artificial neural network model to show how reproductive conflict could lead to the evolution of ritualized display in monogamous species. Although many forms of courtship display are consistent with this hypothesis, it has not, to our knowledge, been empirically tested.

Future directions. The idea that courtship may simply be the product of a manipulative, evolutionary arms race between males and females may initially seem at odds with the entire concept of courtship. However, this novel and compelling hypothesis certainly deserves further study, especially in the context of sexual conflict. Because of obvious limitations in our ability to manipulate variation in the extent and form of elaborate, ritualized pair displays in live birds, observational and comparative investigations of socially

monogamous species present promising avenues for further exploration of this hypothesis. Alternatively, both computer controlled taxidermic models (Patricelli *et al.* 2002) and video manipulation and animation (Turnell *et al.* 2003) hold some promise as a basis for clever experiments to test this idea.

6.3 COPULATION

Like courtship, the copulation behavior of birds is remarkably diverse, with as much as 100-fold or more variation in the duration of coitus, the number of days over which a pair copulates, and the frequency of copulation for a single clutch of eggs. During the past 20 years, much research has been devoted to documenting and understanding this diversity and considerable progress has been made.

6.3.1 Copulation Behavior

6.3.1.1 Ordinary copulation

Normally, birds copulate with the male mounting the female's back, crouching down on his tarsometatarsus, leaning back, and bending his tail and cloaca under the female while the female lifts her tail (Figs. 6.2D,E, 6.17H,I and 6.18A). The pair then makes one to many cloacal contacts (Fig. 6.19), each for a brief period, while the male ejaculates. Many male birds flutter their wings during copulation (Fig. 6.2D,E) and/or hold onto the feathers of the female's head, nape or back with their bill (Fig. 6.17I,L), presumably to maintain their balance and possibly to keep the female from escaping an unwanted copulation.

Within-pair copulations are usually preceded by some form of courtship behavior, as described above, and almost always by solicitation behavior performed by one or both sexes (Figs. 6.2C, 6.17A,C,D,E; Birkhead and Møller 1992). For example, within-pair copulations in the Lapland longspur (*Calcarius lapponicus*) usually begin with the female creeping through the low tundra vegetation, apparently inciting the male (Fig. 6.17B) with a lispy trill (Drury 1961; R. M. unpublished data). Upon seeing this, the male gathers some vegetation in his bill and holds it high while he quivers his wings (Fig. 6.17C). The female then crouches with her tail and head raised, and her wings slightly spread and quivering (Fig. 6.17D). As soon as the female adopts this position, the male drops his load of vegetation and walks toward the female with his bill pointed skyward and his wing tips dragging along the ground (Fig. 6.17E). The male then quickly mounts the female's back, while she twists her tail to the right or left side and the male twists his tail in the opposite direction. The two birds make brief cloacal contact (1-2 s) before the male dismounts. After copulation, the male crouches in front of the female while she raises her head and tail and chatters for a few seconds (Fig. 6.17F).

Because only the left ovary of female is functional in most species, it might be expected that there would be a side bias during copulation (Petersen *et al.* 2001). The entrance to the left oviduct lies on the left side of the cloacal wall, so males might gain some advantage in placing their sperm into the left side of the cloaca and this would be easiest if the male made cloacal contact on the

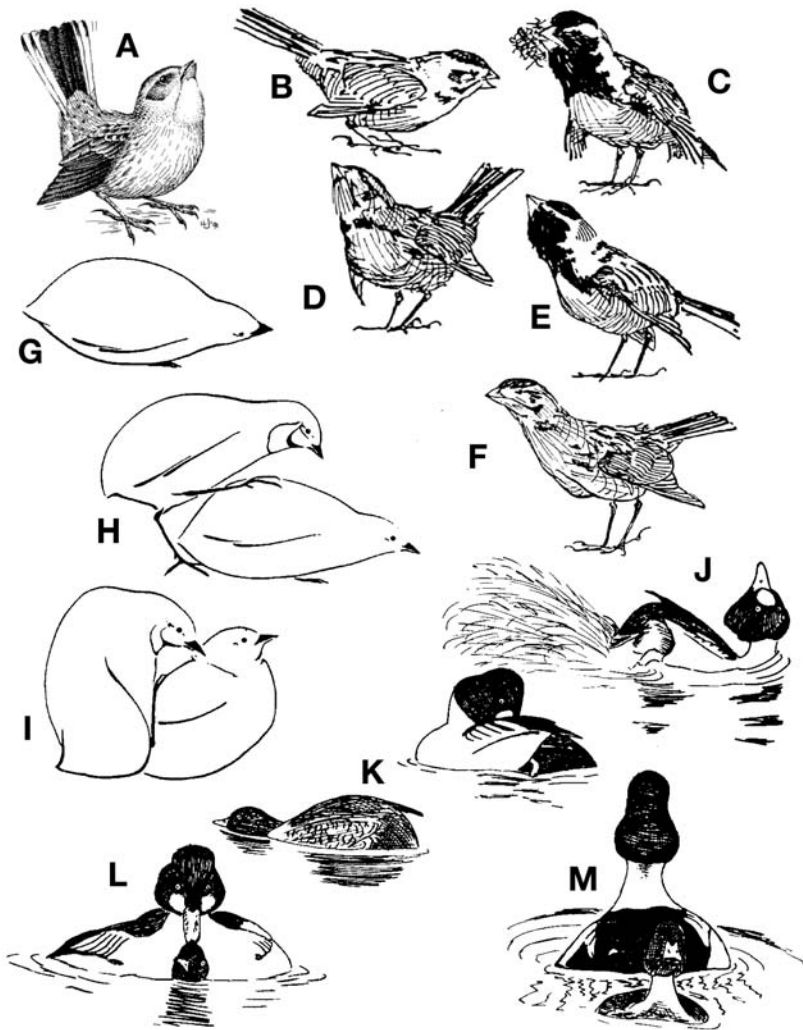


Fig. 6.17 Some examples of typical copulation behavior in birds. **A.** Smith's longspur: female solicitation. Original drawing by Ian Jones. **B-E.** Lapland longspur: female inciting male (B) and solicitation (C); male precopulatory displays, singing quiet song (D), and carrying tuft of vegetation (E); female postcopulatory display (F). Modified after Drury, W. H. 1961. *Bird-Banding* 32: 1-46, Fig. 5. **G-I.** Bluebreasted quail (*Coturnix chinensis*): female solicitation (G), mounting (H), and copulation (I). From Schleidt, W. M., Yakalis, G., Donnelly, M. and McGarry, J. 1984. *Zeitschrift für Tierpsychologie* 64: 195-220, Figs. 41-44; with permission from Blackwell Publishing. **J-M.** Common goldeneye: male Slow Head-throw Kick display (J); female prone on water while male performs Preening-behind-the-wing display (K); copulation (L); and postcopulatory Steaming display (M). Reprinted from Johnsgard, P. A. 1965. *Handbook of Waterfowl Behavior*. Cornell University Press, Ithaca, NY, Figs. 84 and 86; copyright © 1965 by Cornell University; used by permission of the publisher.

left side of the female. A similar argument has been made for the left-bending aspect of the male intromittent organ (IO) in most bird species that have such a structure (Volume 6A, Chapter 3). While there are few data to address this question, Gerhardt (1933) observed that male Ostriches (*Struthio camelus*), which have an IO, mounted females from the left. Similarly, Petersen *et al.* (2001) recorded a significant left side bias for male mounting in the Tree swallow (*Tachycineta bicolor*; Fig. 6.2E) during 69 copulation bouts, where 76% of cloacal contacts ($n = 393$) were from the left. Petersen *et al.* (2001) suggest that females may even be able to bias sperm use by choosing which side to present to the male during copulation. Clearly, there is scope for much more research on this interesting facet of avian copulation.

Though most bird copulate on land in the typical fashion described above, many, but not all, waterbirds copulate on the water. This is true for most ducks, geese, swans, and phalaropes, but not most seabirds (pelicans, boobies, alcids, gulls, terns, penguins, and procellariids), loons, and grebes, all of which copulate on land. In the Common goldeneye (*Bucephala clangula*), which always copulate on the water, within-pair copulations are preceded by a variety of courtship (Fig. 6.17J) and precopulatory displays (Fig. 6.17K) by the male (Eadie *et al.* 1995). When the female is ready to copulate, she stops swimming and flattens herself out on the water surface (Figs. 6.2C and 6.17K) for up to 15 min while the male continues to display. The male then grasps the feathers of the female's nape with his bill and mounts the female, causing her to submerge and almost disappear from view (Fig. 6.17L). Though the male may remain mounted for up to 45 s, coitus averages only 8.3 s, then the male dismounts from the female and performs a postcopulatory display (Fig. 6.17M).

6.3.1.2 Extraordinary copulation

A few bird species have so far been observed to copulate in an unusual manner, compared to the >2000 species known to copulate as described above. Most of these behaviors are so unusual, distinctive, and occurring in distantly related taxa that they are certainly independently evolved, but so far their origins and adaptive significance have been difficult to determine. We summarize seven examples below, based on recent studies, but we realize that there are bound to be others buried in the extensive natural history literature. We expect that many more unusual copulation tactics will come to light when this aspect of the breeding behavior of more species is studied in detail.

Reverse mounting. In all birds, most copulations involve the male mounting the female from above or behind. In most grebes and at least 27 other bird species, however, reverse mounting has been recorded, wherein the female mounts the male (Neuchterlein and Storer 1989). Grebes are especially notable for the high incidence of this behavior. In an intensive study of copulation behavior in Silvery (*Podiceps occipitalis*) and Hooded grebes (*P. gallardoi*) in Patagonia, for example, Neuchterlein and Storer (1989) reported reverse mounting in 27% ($n = 327$) and 15% ($n = 95$), respectively, of observed mounting sequences between the sexes, none of which involved coitus.

Several hypotheses have been proposed to explain this behavior, most of which Neuchterlein and Storer (1989) are able to reject based on their observations. In particular, they argued that the frequency of reverse mounting in these and other grebes suggests that it is not aberrant behavior and must serve some adaptive function. They also reject the idea that reverse mounting results from mistaken sexual identity in these sexually monomorphic birds, as only one same-sex mounting was recorded in their study. Based on several lines of evidence, they concluded that reverse mounting is an integral part of courtship in grebes, suggesting that it may either (i) help to reduce intersexual dominance and aggression or (ii) stimulate development of the female's ovaries.

Sperm ejection. In the Dunnock (*Prunella modularis*), feral domestic fowl (*Gallus gallus domesticus*), and Black-legged kittiwake (*Rissa tridactyla*), females regularly eject sperm from their cloaca as part of the normal copulation sequence, though each species does this for different reasons. In the Dunnock, unlike most other passerines, there is an elaborate display immediately preceding copulation (Davies 1983). The female crouches, fluffs her body feathers, quivers her wings and tail, and raises her tail so that her cloaca is visible while the male hops from side-to-side behind her and pecks at her cloaca for up to 2 min before he mounts and copulates. The female's cloaca becomes pink and distended from the male's pecking and often makes a pumping action during which sperm is ejected. Because females copulate with more than one male for a clutch of eggs, Davies (1983) suggested that cloaca-pecking might be driven by sperm competition if the sperm of rival males is ejected (see also Chapter 7).

Female feral fowl seem to prefer to copulate with dominant males but are often coerced into copulation with subordinate males (Pizzari and Birkhead 2000). When this happens, females are more likely to eject the sperm from their cloaca immediately after copulation, and before the coercing male dismounts. Pizzari and Birkhead (2000) were able to confirm this result by experimentally manipulating male dominance, and showed that about half of the inseminated sperm could be ejected by the female. Thus, by sperm ejection, females would be able to bias the paternity of their offspring towards the more-favored, dominant males (Pizzari and Birkhead 2000).

In the Black-legged kittiwake, females eject sperm from their cloaca after copulations at a rate that declines steadily to zero, beginning about two weeks before egg-laying begins (Wagner *et al.* 2004). Since this species is both socially and sexually monogamous, Wagner *et al.* (2004) argued that females preferred fresh (young) sperm to fertilize their eggs, and, indeed, showed that chicks hatched from eggs fertilized from older sperm were in poorer condition than those hatched from younger sperm. Thus sperm ejection in this species appears to have nothing to do with sexual selection and sperm competition but is instead favored by natural selection for increased egg hatchability and offspring condition.

Copulation without mounting. Though many species in the family Alcidae (auks, puffins, murrelets) copulate on land in the normal fashion, four species of auklet have been recorded to copulate in an unusual manner on the sea (Hunter and Jones 1999). In the Least (*Aethia pusilla*), Crested, Whiskered (*A. pygmaea*), and Parakeet (*Cyclorhynchus psittacula*) auklets, the male does not mount the female's back but instead approaches her from the rear as she sits on the water. The male then raises himself almost vertically by flapping his wings, bringing his cloaca up under the female's raised tail to contact her cloaca out of the water (Fig. 6.18C). The male maintains this position by vigorously flapping his wings and using his feet to balance himself for 3-5 s (Ian Jones and Fiona Hunter, personal communication). The remaining four alcids (the three puffins, *Fratercula* spp., and the Marbled murrelet, *Brachyramphus marmoratus*) known to copulate on the water probably use the same method. As Hunter and Jones (1999) argue, this unusual form of copulation may be an adaptation to reduce water damage to the sperm, which might ensue if the female's cloaca was submerged during cloacal contact (Volume 6A, Chapter 3).

Face-to-face copulation. Unlike any other bird studied to date, the New Zealand stitchbird (*Notiomystis cincta*) has two very different copulation behaviors (Anderson 1993). During unforced, within-pair copulations, the

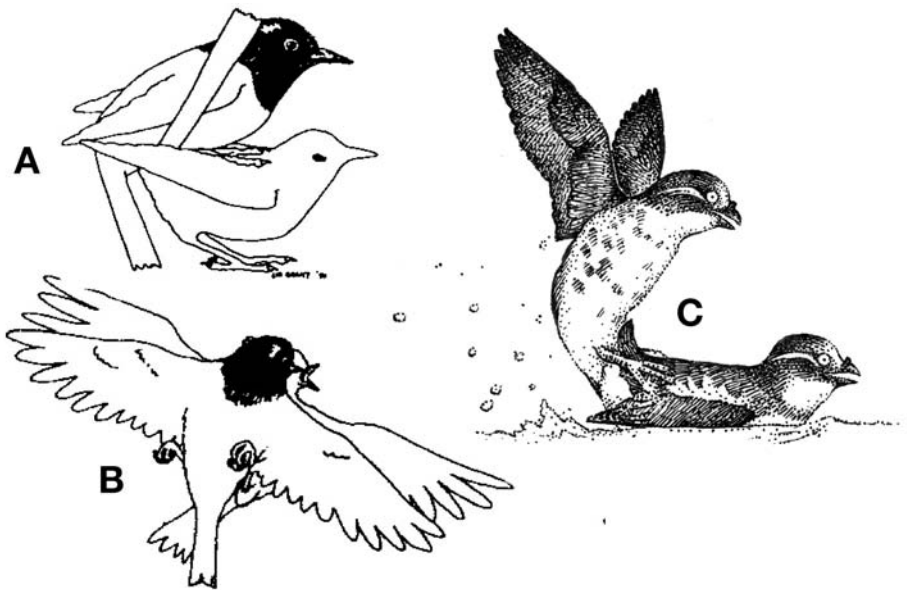


Fig. 6.18 Some examples of extraordinary copulation behavior in birds. **A, B.** New Zealand stitchbird: within-pair, standing copulation (**A**), and forced, extrapair, face-to-face copulation (**B**). From Castro, I., Minot, E. O., Fordham, R. A. and Birkhead, T. R. 1996. Ibis 138: 765-771, Fig. 4; with permission from Blackwell Publishing and the authors and artist **C.** Crested auklet: aquatic copulation without mounting. Original drawing by Ian Jones.

male always stands on the female's back and copulates in a fashion similar to that of most other birds, as described above (Low 2005). Thus, the male and female approach each other and mutually rub each other's necks while vibrating their wings. Then, when she is ready, the female turns and the male hovers onto her back while she moves her tail to the side, and they briefly press their cloacas together (Fig. 6.18A). Following coitus, the male dismounts, sometimes rubs necks again with the female, then calls and flies away (Low 2005). During forced extrapair copulations (EPCs), however, the male copulates face-to-face with the female (Fig. 6.18B), after chasing her to the ground while she emits a series of distinctive, high-pitched distress calls. The male then forces the female onto her back, positions himself on top of her, grasping her legs with his feet and using his outstretched wings (Fig. 6.18B) to control his balance and prevent the female from escaping. Males then often peck the female's head and neck as she vigorously struggles to escape (Castro *et al.* 1996; Low 2005). In only 3 of 28 instances of this type of copulation was the female observed to escape without cloacal contact (Low 2005).

In one study population (Low 2005), all forced copulations were extrapair and occurred during intrusions on another male's territory. Forced EPCs often involved up to 7 other males engaged in chasing the female, though only one of these eventually caught and copulated with the female. Twenty-eight of 39 forced EPCs were face-to-face (Fig. 6.18B), whereas the remaining 11 were in the normal 'standing' position (Fig. 6.18A), and in all of these forced copulations the female emitted the distinctive distress calls. During standing, forced EPCs, the male performed an abbreviated pre-copulatory display (briefly neck-rubbing) but never called on dismounting. Pair males were sometimes attracted by the female's distress calls, whereupon they approached and chased the intruding male away. Of 8 cases of EPCs where the female appeared to consent, only one was face-to-face. Thus, face-to-face-copulation is clearly associated with both forced and extrapair copulations.

While face-to-face copulation appears to be unique in the New Zealand stitchbird, it is relatively easy to imagine how it might have evolved. Many birds fight face-to-face, grappling with their feet and pecking with their bill, so it is maybe a little surprising that this form of copulation has not been recorded during forced EPCs in other species. Interestingly, the cloacal protuberance (Volume 6A, Chapter 3) of the male New Zealand stitchbird enlarges and changes orientation during the breeding season, angling about 60° further towards the bird's head so that it is perpendicular to the abdomen rather than pointing towards the rear (Fig. 6.20A). While this change in the orientation of the CP appears to facilitate face-to-face copulation, it probably also facilitates normal copulation (Fig. 6.20B) and is found in other bird species (Low 2005).

Prolonged intromission. Both the Greater (*Coracopsis vasa*) and Lesser vasa parrot (*C. nigra*) from Madagascar, the Comoro Islands, and the Seychelles have an intromittent organ (IO; see Volume 6A, Chapter 3) that dramatically influences their copulation behavior. As far is known, none of the other

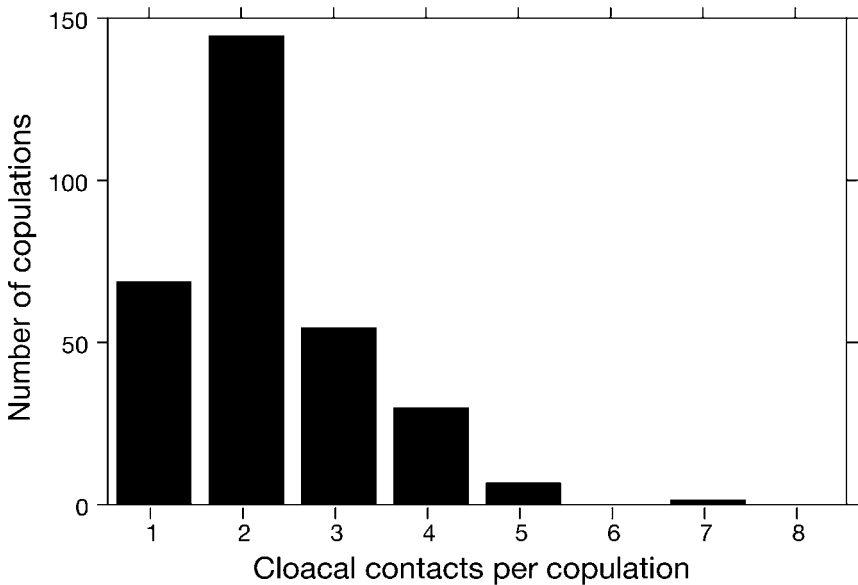


Fig. 6.19 Number of cloacal contacts per copulation event in Alpine accentors (*Prunella collaris*). Modified after Davies, N. B., Hartley, I. R., Hatchwell, B. J. and Langmore, N. E. 1996. *Animal Behaviour* 51: 27-47, Fig. 5c.

9000+ species of Neoaves have an IO (Volume 6A, Chapter 3), so it seems quite likely that this form of copulation is unique.

Copulations were described in detail by Wilkinson and Birkhead (1995) who observed the behavior of a female and two male Greater vasa parrots in a zoo during the breeding season. To initiate the single copulation observed in its entirety, the female pursued the males until she came to perch beside one of them. The male then leapt over the female's back several times before landing on her and immediately making cloacal contact and intromission of the male's large, fleshy cloacal protrusion (Volume 6A, Chapter 3). The male then stepped off the female but their cloacas remained interlocked with the male's tail curled under the female's, and the female's right wing extended over the male. When the female began to preen and grasp the male's nape, he began vigorous copulatory thrusting. After 15 min of intromission the female periodically took regurgitated food from deep within the male's bill, and called between these feeding bouts. The pair remained in coitus for 104 min, after which both sexes ejected a small volume of fluid (semen?) from their everted cloacas. Five other copulations observed in progress were estimated to have involved intromission for >100 min each (Wilkinson and Birkhead 1995). Anecdotal observations suggest that the Lesser Vasa Parrot has similarly prolonged copulations involving their cloacal protrusion (Wilkinson and Birkhead 1995).

Avian orgasm. Like the vasa parrots, Red- and White-billed buffalo weavers (*Bubalornis niger* and *albirostris*) of sub-Saharan Africa have an unusual

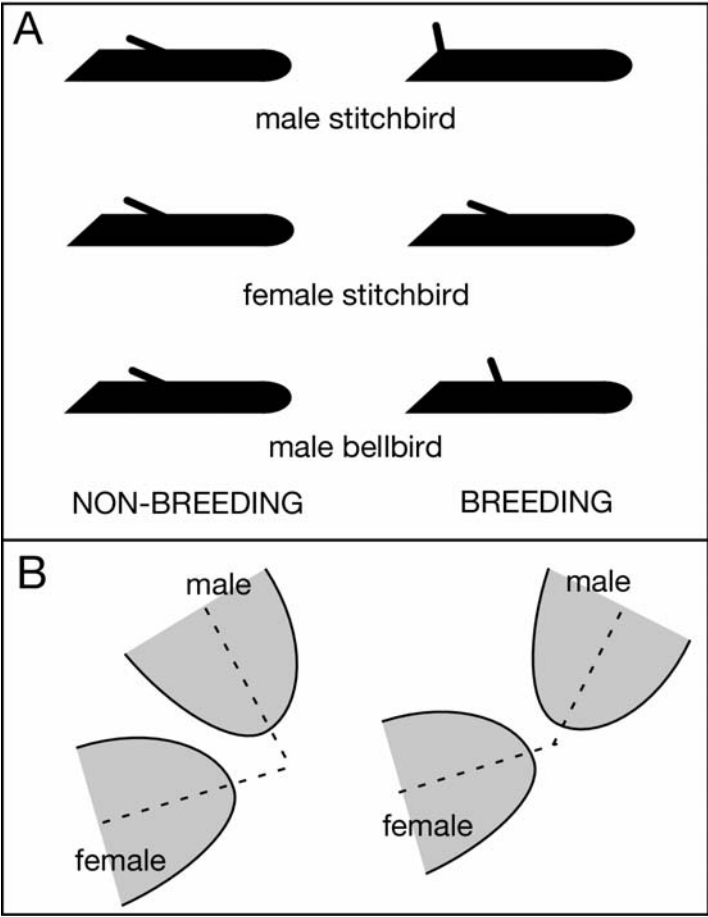


Fig. 6.20 **A.** Orientation of the cloacal protuberance in New Zealand stitchbirds and Bellbirds (*Anthornis melanura*) in breeding (left) and non-breeding (right) seasons, drawn as if lying on their backs with their heads to the right. **B.** Presumed relative positions of male and female protuberances during face-to-face copulations in New Zealand stitchbirds showing how they would align if there was (right) or was not (left) a change in the angle of the protuberance during the breeding season. Modified after Low, M., Castro, I. and Berggren, Å. 2005. *Behavioral Ecology and Sociobiology* 58: 247-255, Table 2 and Fig. 3.

copulatory structure (Volume 6A, Chapter 3) that makes their copulation behavior extraordinary (Winterbottom *et al.* 1999, 2001). Unlike the vasa parrots, though, the phalloid organ of male buffalo weavers is not intromittent, but is instead rubbed against the female's cloacal region during copulation (Winterbottom *et al.* 1999). Based on observations of Red-billed buffalo weavers in both the field ($n = 6$) and an aviary ($n = 57$), Winterbottom *et al.* (1999) report that copulations begin in the typical fashion with the male mounting the female's back. However, as the copulation proceeds, the male

leans backwards away from the female and flaps his wings vigorously while rubbing his phalloid organ against the female. During the final moments of copulation, males seem to experience an 'orgasm' as their wingbeats slow to a quiver and their body shakes, with their leg muscles apparently in a spasm. During this 'orgasm', the male clenches the female with his feet and pulls her closer. In the aviary, where males mated with a model female ($n = 34$), semen was found in the model's cloaca only when the male displayed this orgasm-like behavior (Winterbottom *et al.* 1999). Copulation sequences were prolonged (mean = 18 min, range 4-30 min in the field; 29 ± 0.76 min in the aviary) and alternated between bouncing displays by both sexes and mounting as described here. Winterbottom *et al.* (1999) present fairly clear evidence that both mounting and rubbing of the phalloid organ are necessary for ejaculation. Although a few other birds have a non-intromittent phalloid organ (Volume 6A, Chapter 3), no other bird species appears to rub it against the female in this fashion, or exhibit orgasm-like behavior.

Aerial copulation. There are many reports of swifts (family Apodidae) copulating in the air but there is only anecdotal evidence that these aerial interactions involve coitus and sperm transfer. The Chimney swift (*Chaetura pelagica*), for example, often engages in aerial courtship displays and occasionally the male approaches the female from above and behind while performing a V-display with wings held rigid in a V above the back (Cink and Collins 2002). The male then thrusts his body forward to make brief contact with the female without moving his wings, apparently copulating. Like other swifts (e.g., Marín 1997), Chimney swifts also grapple together in the air and tumble towards the ground, and this too has sometimes been interpreted as copulation. Most often, though, copulation occurs at the nest site in the Chimney swift, with the male crawling and fluttering onto the female's back and maintaining coitus for 2-4 s (Cink and Collins 2002). While swifts are certainly agile enough to copulate in the air, more detailed observations, and possibly experiments, are needed to determine whether birds actually make cloacal contact and transfer sperm during aerial displays. Marín (1997), for example, argues these apparent copulations may instead be a form of agonistic behavior.

In the American dipper (*Cinclus mexicanus*), copulations have also been recorded as occasionally occurring in the air (Kingery 1996). Similar reports of aerial copulation in the Least flycatcher (*Empidonax minimus*; Tarof and Ratcliffe 2000) are almost certainly mistaken (J. Briskie, personal communication) and all reports of aerial copulation in birds need to be carefully documented to distinguish these interactions from other forms of courtship and aggression.

6.3.2 Timing of Copulation

6.3.2.1 Introduction

Even among the few hundred bird species studied in depth so far, there is incredible diversity in the frequency and timing of copulations from one to

hundreds of copulations per clutch, and from one day per year to virtually every day and every hour of daylight during the breeding season in some species. In more than 15 years of research in the Canadian arctic, for example, we have never observed White-rumped sandpipers (*Calidris fuscicollis*) to copulate (R.M. unpublished data), despite their highly visible courtship displays (Fig. 6.8B), occasional attempts at mounting, and detailed round-the-clock observations during the continuous daylight of the high arctic summer. On the other hand, Red phalaropes (*Phalaropus fulicarius*) at our study site could be seen copulating at any time of day during the courtship period, with minimal attention and effort on our part (R.M., unpublished data). Understanding all of this diversity has been a challenge, though considerable progress has been made, particularly in the context of sperm competition (Birkhead *et al.* 1987; Birkhead 1998). In this and the next section, we attempt to bring those previous reviews up-to-date and add some new perspectives that may help guide future research.

6.3.2.2 Seasonal patterns

In the New Zealand stitchbird, within-pair copulations begin about a week before the first egg in a clutch is laid and continue until the clutch is completed, with the peak copulation rate occurring 2 d before clutch initiation (Fig. 6.21A; Low 2005). This is a fairly typical pattern in birds (Fig. 6.21A,D,E,F) and is the sort of schedule that might be expected given both the mechanics of sperm storage and fertilization and some threat of sperm competition from extrapair males (Birkhead *et al.* 1996; Birkhead 1998). Nonetheless, this pattern is far from universal even for within-pair copulations, so we have attempted to summarize the known patterns into three broad categories that may have some internal consistency with respect to their adaptive functions, as follows.

Contracted pre-clutch copulations. In some species, copulations are rare and occur only in the few days before the laying of the first egg in a clutch. In the American redstart, for example, there are few within-pair copulations (as few as one) and these always occur towards the end of the nest-building period, before the laying of the first egg (Sherry and Holmes 1997; R. Norris personal communication). This pattern of copulations is expected when (i) only a few copulations are needed to supply the female with enough sperm to fertilize an entire clutch of eggs, (ii) copulations with other males have not occurred within the month or so before clutch initiation, and (iii) the copulations occur when the sperm can be stored in the females sperm storage tubules (SSTs; Volume 6A, Chapter 4) for the duration of egg laying. The first condition seems always to be true as, in all birds that have been studied so far, ejaculate size is far more than sufficient to fertilize even the largest clutch. Only when there is some variability in sperm viability (Morrow *et al.* 2002), or when coitus does not result in sperm transfer to the female, should more than one copulation be required.

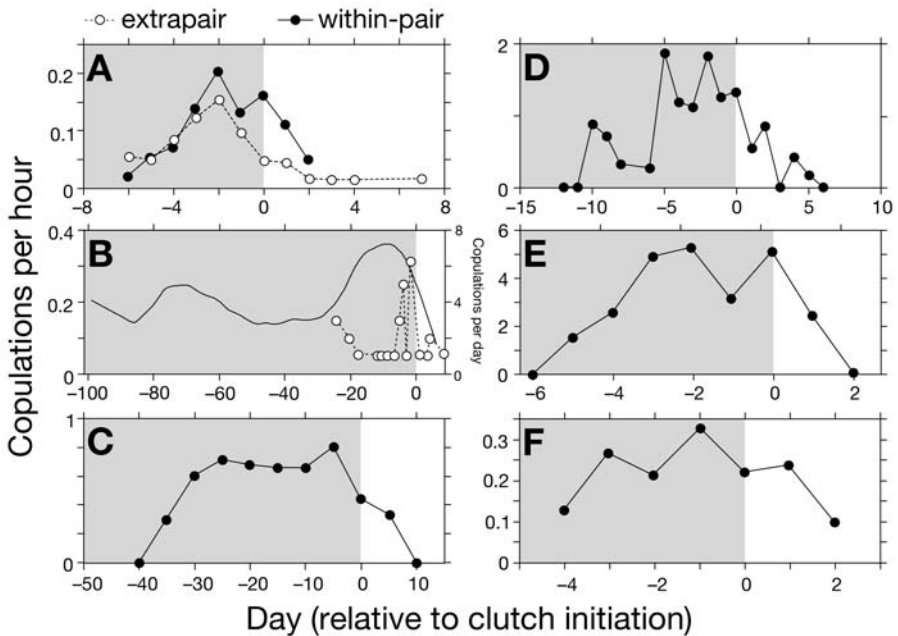


Fig. 6.21 Seasonal timing of copulations relative to the initiation of egg laying in species with a variety of social and sexual mating systems; period before egg-laying is shaded. **A.** New Zealand stitchbird ($n = 58$ within- and 77 extrapair copulations). Modified after Low, M. 2005. *Journal of Avian Biology* 36: 436-448, Fig. 1. **B.** Lesser kestrel; mean within-pair copulation attempts per hour in pairs more than 1 year old (smoothed using LOWESS) and extrapair copulation attempts per day involving paired females. Modified after Negro, J. J., Donazar, J. A. and Hiraldo, F. 1992. *Animal Behaviour* 43: 921-930, Figs. 1 and 4. **C.** Osprey; mean within-pair copulation attempts for 23 pairs. Modified after Mougeot, F., Thibault, J.-C. and Bretagnolle, V. 2002. *Animal Behaviour* 64: 759-769, Fig. 1a. **D.** Bearded tit (*Panurus biarmicus*); means for 8 pairs nesting with other males present. Modified after Sax, A., Hoi, H. and Birkhead, T. R. 1998. *Animal Behaviour* 56: 1199-1204, Fig. 1b. **E.** Smith's longspur; means of 6 females observed each day. Modified after Briskie, J. V. 1992. *Auk* 109: 563-575, Fig. 4. **F.** Spotted sandpiper (*Actitis macularia*); means from 14 females over 3 years. Modified after Oring, L. W., Reed, J. M. and Maxson, S. J. 1994. *Animal Behaviour* 47: 1065-1072, Fig. 1.

The second condition obtains because females can store sperm for up to 45 d in their SSTs (Volume 6A, Chapter 3). Although sperm appears to leak out of these tubules at a more-or-less constant rate (Colegrave *et al.* 1995), it is always possible that sperm stored from a previous copulation within a month or so of egg-laying will fertilize an ovum, although the probability of fertilization should depend upon the time since that previous copulation, the seasonal pattern of SST growth and maintenance (Briskie 1994), and the total amount of sperm inseminated and stored from the pair male (Colegrave *et al.* 1995). Interestingly, extrapair fertilizations are common in the American redstart

(Sherry and Holmes 1997), but pair males copulate very little, an apparent exception to the general pattern.

The third condition is influenced by the mechanics of sperm storage, fertilization, and egg laying in birds (Volume 6A, Chapters 4, 6, and 10). Almost all fertilizations in birds likely result from sperm stored in the female's SSTs rather than from sperm moving to the infundibulum directly from the cloaca following an insemination (R. M. unpublished data). Thus sperm that does not enter the SSTs is probably removed from the cloaca during defecation (Immler and Birkhead 2005) and egg laying (K. Persaud and R. Montgomerie unpublished data). In addition, in at least some species, SSTs are only available and able to store sperm for a short period before egg laying begins (e.g., Briskie 1994), so inseminations that occur before this period are almost certainly unable to fertilize ova.

Extended clutch copulations. In many species (e.g., the New Zealand stitchbird described above), copulations extend from several days before until a few days after the egg-laying period (Fig. 6.21A,D,E,F). This pattern is almost certainly driven by the average frequency of extrapair copulation (EPC) in the population and thus by the threat of extrapair paternity. Given that the timing of copulations with respect to egg laying, the insemination window, and last male sperm precedence influence the probability of fertilization (Colegrave *et al.* 1995; Birkhead 1998), it is not surprising that the frequency and uncertainty of extrapair copulations influences the timing of within-pair copulations in this fashion.

Extended courtship copulations. Probably the most unusual, and poorly understood seasonal pattern of within-pair copulations occurs in species that copulate for extended periods, far outside the interval when inseminations could possibly fertilize ova for the next clutch of eggs (Fig. 6.21B,C). For example, in the Lesser kestrel within-pair copulations begin as many as 120 d before the laying of the first egg and show two peaks in copulation rate; one at about 65 d and the other about 5 d before clutch initiation (Fig. 6.21B; Negro *et al.* 1992). The first period of copulation peaking at 65 d before clutch initiation is well before any stored sperm would be likely to survive long enough to be able to fertilize the first ovum that the female releases, so cannot be adaptive by contributing directly to fertilization success. At least a dozen other species have so far been found to copulate outside the period when stored sperm would be likely to fertilize an ovum (Birkhead and Møller 1992). Several hypotheses have been proposed to explain this extended period of copulation but most of these also apply to frequent copulations as well (see below). Here we discuss three hypotheses that might explain the long period of copulation, even in the absence of high copulation frequency.

First, early copulation may be a form of mate guarding. Copulations (and courtship) may, for example, keep a female from straying into other males' territories during the period of pair formation when she is sexually active but not ready to begin a clutch. Similarly, if copulations are initiated by the female,

they could keep the pair male's sperm depleted and render him less likely to seek extrapair matings. This hypothesis is usually discussed in the context of copulation frequency but it could apply independent of high copulation rates. However, there is currently no empirical data that would suggest that it does.

Second, it has been suggested that males initiate copulations early simply because they are uncertain about the period of female fertility and are hedging their bets. While this is certainly plausible, it cannot explain why all birds do not make this mistake, especially those with long periods of courtship before egg laying begins. Even within the Falconiformes, with many species showing extended periods of copulation, some species restrict copulations to just before clutch initiation.

Finally, it is possible that an extended copulation period is simply the result of copulations forming an integral part of courtship. Thus, copulations that occur long before the period when the female can be fertilized may serve the same functions as other aspects of courtship behavior discussed earlier; advertising quality, coordinating reproductive cycles, etc. It is also possible that such early copulation is just a correlated response to selection for early courtship that raises testosterone levels and thus makes males more interested in copulation. All of the available evidence seems to point to this general hypothesis being the most likely explanation. In Lesser kestrels, for example, the onset of copulation coincides with the return to the colony and the beginning of courtship (Negro *et al.* 1992), with the early peak possibly coinciding with heightened courtship during pair formation.

6.3.2.3 Diel patterns

Most species studied in detail so far have a diel pattern of copulations usually peaking in frequency soon after dawn (Fig. 6.22), and, in some species, late in the daylight hours as well. Copulation early in the day usually occurs within an hour or two after the laying of an egg, and has often been interpreted as coinciding with the insemination window of the female. Copulations late in the day during the egg-laying period, as occur in the Lesser Kestrel (in addition to early morning copulations), may thus occur too late relative to this insemination window to have any chance of fertilizing an ovum. In these cases, late-day copulations may be a component of the species' courtship behavior, as Negro *et al.* (1992) suggested for Lesser kestrels, as these copulations occur soon after the pair meets up at the colony after a day of foraging.

The insemination window is the period when a copulation during the egg-laying period is most likely to lead to sperm storage and subsequent fertilization, because inseminations that occur outside this window are likely to be swept out of the oviduct or cloaca as the egg passes down from the infundibulum (Birkhead 1998). Semen from copulations in the hour or two before an egg is laid is probably still in the cloaca or vagina on its way to the SSTs, and would be swept away as the shelled egg passes by. Sperm from copulations following the laying of an egg can make it to the SSTs but any

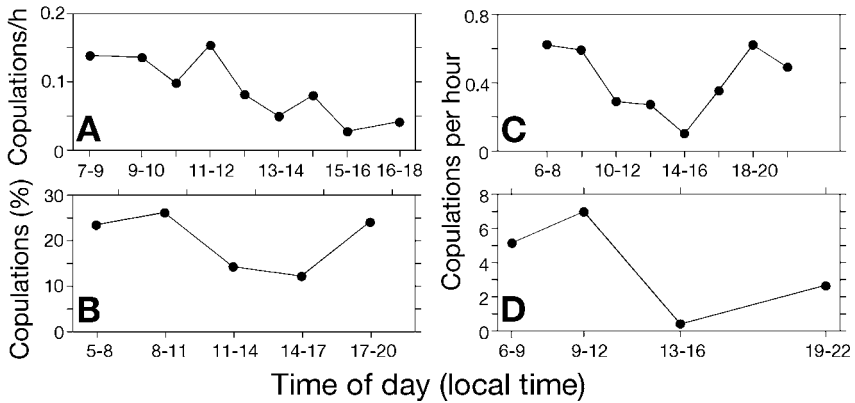


Fig. 6.22 Diel timing of copulations. **A.** New Zealand stitchbird; within-pair copulations (n = 58) observed per hour. Modified after Low, M. 2005. Journal of Avian Biology 36: 436-448, Fig. 2. **B.** Northern goshawk; mean percent of copulations observed for two pairs during each time period. Modified after Rutz, C. 2005. Ibis 147: 831-835, Fig. 1b(ii). **C.** Aquatic warbler (*Acrocephalus paludicola*); copulations (n = 31) by two pairs in captivity. Modified after Schulze-Hagen, K., Leisler, B. and Birkhead, T. R. 1995. Ibis 137: 85-91, Fig. 5. **D.** Smith's longspur; means from 6 females. Modified after Briskie, J. V. 1992. Auk 109: 563-575, Fig. 5.

sperm that has left the SSTs en route to the next unfertilized ovum available at the infundibulum has probably only 1-2 hours available before the next fertilized ovum starts to make its way down the oviduct, taking with it any sperm in its path. There are certainly bound to be variations on this pattern depending upon the inter-egg interval, but this scenario probably applies to most species, where laying eggs at 24-h intervals is the norm. Recent experimental evidence from Japanese quail is entirely consistent with this description (K. Persaud and R. Montgomerie unpublished data), but more work is needed from other species to confirm its generality, particularly for species that lay eggs at intervals other than 24 h.

The Australian brush turkey (*Alectura lathami*) is a striking exception to this general pattern in that the majority (61%) of within-pair copulations occur less than an hour before an egg is laid (Birks 1999). In this species, females lay one egg every few days, in huge mounds of rotting vegetation tended by the males. When a female arrives at a mound ready to lay an egg, she usually solicits her first copulation within 2-3 min, and lays the egg on average 37 min (range 8-94 min) later. To have any chance of fertilizing an ovum, these pre-laying inseminations would need to move to the SSTs to avoid being swept out of the cloaca as the egg is laid. During that brief period between insemination and egg-laying, the egg that is about to be laid would have to be higher in the oviduct than the uterovaginal junction where the SSTs reside. All of this is possible, though there are no data available to test this idea. The timing seems crucial because the female departs the mound immediately after briefly covering the egg, leaving the male to bury and care for the egg until it hatches

7-10 weeks later, and thus providing no opportunity for copulation immediately after laying the egg. This copulation scenario is thus entirely under the control of the female who appears to be paying (with a copulation and potential fertilization) for the privilege of laying her egg in the male's mound (Birks 1999). The remaining (39%) within-pair copulations occur when a female visits a male's mound outside the context of egg-laying and may, in fact, be responsible for all fertilizations (Birks 1999). Certainly, both kinds of copulations make some sense in the context of sperm competition but more work will be needed to determine the relative efficacy of, and reasons for, the copulations that immediately precede the laying of an egg.

6.3.3 Duration of Copulation

Based on data from a few well-studied species, we know that a male can transfer an ejaculate to a female in less than 3 s of cloacal contact. For example, a single copulation of this duration in Zebra finches (*Taeniopygia guttata*), feral fowl, and Japanese quail under controlled experimental conditions transfers enough sperm to the female to fertilize ova for many days thereafter (Birkhead *et al.* 1995; Adkins-Regan 1995). Moreover, more than 30% of species that have been studied in the wild copulate for less than 5 s (Fig. 6.23; Birkhead *et al.* 1987) and this percentage is almost certainly an underestimate, for several reasons. First, the data on which that estimate is based is largely anecdotal, from field observations of behavior that were not precisely timed. Second, many observers did not distinguish between mounting and actual coitus. Third, in many species, what looks like a single cloacal contact is actually repeated contacts (Fig. 6.19), and possibly repeated ejaculations. Finally, it is quite likely that this sample is biased toward long copulations as these are the most likely to be recorded, either because they are out of the ordinary or are simply more likely to be observed in the field.

Even so, many bird species copulate for >5 s (Fig. 6.23), and several hypotheses have been proposed to explain these longer durations. First, while addressing a different question, Wesolowski (2001) proposed that a male with an intromittent organ (IO) would take longer to copulate than a male without one. The available data (Volume 6A, Chapter 3) do not support this hypothesis. Second, Birkhead and Møller (1992) suggested that the duration of coitus might be influenced by the size of the ejaculate, reasoning that larger ejaculates would take longer to transfer from male to female. Since larger males are expected to have larger ejaculates (Møller 1988), there should be a relation between male size and the duration of copulation. Such a correlation has been reported (Birkhead *et al.* 1987) but it was not statistically significant and the apparent pattern may be confounded by other variables as described in the remaining hypotheses. Moreover, there is as yet not enough information on interspecific variation in ejaculate size to test this hypothesis rigorously.

Third, the duration of coitus might be influenced by the risk of predation (Birkhead *et al.* 1987), with pairs under such risk breaking off coitus before the

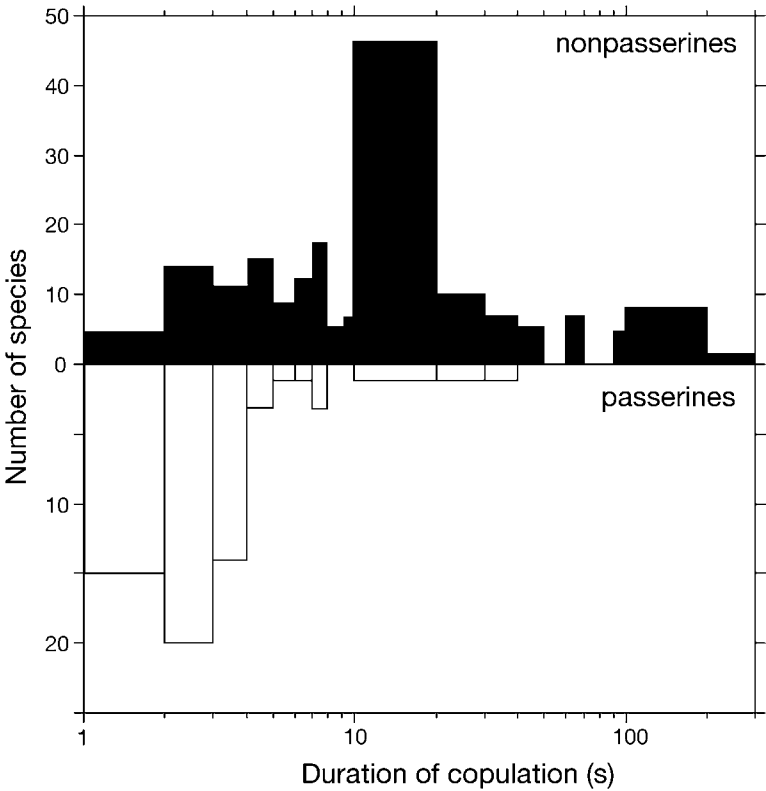


Fig. 6.23 Copulation duration in a sample of non-passerine (mean 10.7 s, $n = 183$) and passerine (mean 2.6 s, $n = 60$) bird species. Non-passerines copulate for significantly longer than passerines (ANCOVA, $F_{1,240} = 28.8$, $P < 0.0001$), controlling for the significant effect of male body mass ($F_{1,240} = 8.3$, $P = 0.004$). Note that copulation duration is plotted on a log scale. Original data.

male is able to transfer all of the semen that he has available, or before the termination of coitus would be optimal for other reasons, as described below. Birkhead *et al.* (1987) tested this idea by comparing the duration of copulation between colonial- and solitary-nesting species, but found no difference. It might be argued, however, that predation risk does not differ substantially between these groups, and that other factors confound this comparison. Birkhead *et al.* (1987) also compared the copulation duration of large and small birds, arguing that large birds should have higher predation risk. Controlling for potentially confounding variables (coloniality and body size), they found no support for this hypothesis either.

Fourth, Birkhead *et al.* (1987) proposed that most of the variation in copulation duration may be the result of mechanical constraints that make maintaining coitus difficult for some species. They argued, for example, that small birds may simply be more agile than larger ones, and that this pattern would explain the correlation with body size. Note, however, that this

explanation may explain much of the variation in copulation (mounting, coitus, and dismounting) duration but is unlikely to account for much variation in coitus duration. It might be expected that copulation with an IO is mechanically more difficult than copulation without one. Alternatively, it might be argued that copulation with an IO is mechanically easier than copulation without one since the male has more opportunity to force a copulation (Volume 6A, Chapter 3), not requiring the female to hold her cloaca against the male's for semen transfer. Nonetheless, the presence of an IO does not influence the duration of a copulation when controlling for body size (Volume 6A, Chapter 3). Interestingly, non-passerines have significantly longer copulations than passerine birds (Fig. 6.23) when controlling for both body size and the presence of an IO, possibly suggesting that a mechanical difference might be responsible. More work is needed to test this hypothesis and to elucidate the mechanisms underlying the pattern.

Finally, we suggest that the duration of coitus may simply be related to the duration of semen transfer, even when controlling for body size and ejaculate size. Since most birds lack an IO (Volume 6A, Chapter 3), female cooperation is necessary for the successful transfer of semen to the female's cloaca, and particularly to the opening of the female's left vagina in the wall of the cloaca (Volume 6A, Chapter 9), which would increase the male's chance of sperm storage and fertilization. If this hypothesis is correct, successful forced copulations should involve longer periods of coitus than unforced copulations, and males that copulate with females that have multiple copulation partners should, on average, engage in coitus for longer periods. Quantitative data are sorely needed to test this hypothesis.

6.3.4 Frequency of Copulation

6.3.4.1 Frequency

There has probably been more attention given to the frequency of copulation than any other aspect of copulation behavior, probably because many species copulate so much more than would seem necessary for successful fertilization, even in the face of sperm competition. At the high end of the spectrum of copulation frequency in birds is the Smith's longspur (*Calcarius pictus*) with up to 600 or more copulations per clutch of eggs, all within 10 d prior to the laying of the penultimate egg in a clutch (Briskie 1992). Peak copulation rate occurs at clutch initiation, averaging 5.3 copulations per hour (Briskie 1992), but is sometimes as high as 19 copulations/h for a given female (R.M. unpublished data). Smith's longspurs have an unusual, polygynandrous mating system, but at any one time there is usually only one male associated with a female (Briskie 1992). At the other end of the spectrum, American redstart pairs copulate only a few times per clutch even though sperm competition seems to be intense in this species, with 40% of nestlings sired by extrapair (usually neighboring) males (Sherry and Holmes 1997). The challenge, then is to understand why in some species we see only a few

copulations per clutch whereas in others hundreds of copulations per clutch are the norm (Fig. 6.24).

Five hypotheses have so far been suggested to explain this variation, and we add a sixth one here. Frequent copulation is not just a feature of some bird species and so these can and have been tested in other taxa as well (e.g., Stockley and Preston 2004). In each case we briefly describe the hypothesis and some evidence in support of it, but we refer the reader to past reviews for more details (Birkhead *et al.* 1987; Birkhead and Møller 1992; Birkhead 1998). Note that some of these hypotheses are related to the reasons we have enumerated both for the seasonal timing of copulation and for courtship behavior in general.

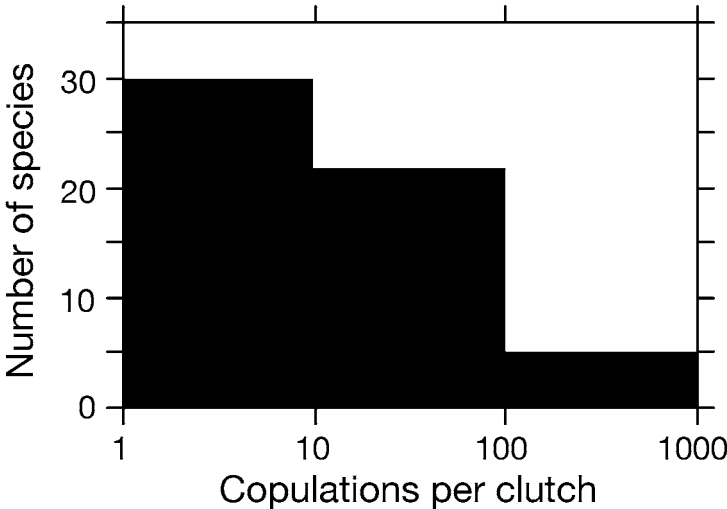


Fig. 6.24 Frequency of copulation in birds. Modified after Birkhead, T. R. and Møller, A. P. 1992. *Sperm Competition in Birds: Evolutionary Causes and Consequences*. Academic Press, London, Fig. 8.1.

H1 Courtship (pair bond formation). It has been suggested that, in some species like the Lesser kestrel, frequent copulation over a long period is simply the result of copulations being part of the courtship display as they occur too early in the breeding cycle to fertilize ova. This is a reasonable suggestion but very difficult to test, as noted above, and especially hard to disentangle from the potential mate-guarding role of copulations.

H2 Mate guarding. As suggested for courtship behavior in general, copulations outside the period of female fertility might serve some mate-guarding function. Certainly the frequent copulations over a long period in the colonial seabirds supports this view.

The Smith's Longspur presents an interesting example in this regard as it is the female who solicits copulation (Fig. 6.17A; Briskie 1992). Thus, the high copulation rate in this species might be a way for females rather than males to

guard their mates. In this species, males tend their broods in proportion to their perception of their paternity (Briskie *et al.* 1998) and probably use the number and timing of copulations with each female as an index. Thus it is to a female's advantage both to increase a male's perception of his relative paternity in her clutch and to keep him from copulating with other females while he is consorting with her, thus lowering his perception of paternity in the clutches of those other females.

H3 Mistaken timing. If males are uncertain about when their mate(s) will initiate egg-laying, it would pay them always to copulate as if there was going to be an ovum ready to fertilize within the next 48 h or so. This idea will be difficult to disentangle from mate-guarding by the female, as concealed ovulation provides a clear advantage to females. At least in seasonal breeders, where the timing of breeding is critical to maximizing food availability and/or minimizing predation risk, it is difficult to imagine that males would not be able to use other cues to indicate when breeding is about to begin, even if pair formation occurs much earlier.

H4 Sperm competition. For the past 15 years or so, sperm competition (including mate guarding) has been by far the most widespread and compelling explanation for frequent copulation in birds. This hypothesis is based on the logic of delivering large and frequent amounts of sperm, as well as vying for last male advantage, to maximize fertilization success under sperm competition (Birkhead and Møller 1992). If this hypothesis is correct, we would expect (i) a positive relation between copulation rate and extrapair paternity (Hunter *et al.* 1993), (ii) higher copulation rates in species where mate guarding by close following is constrained by foraging and other activities (Birkhead *et al.* 1987), and (iii) a positive relation between copulation rates and testis size (an index of sperm competition), though clearly testis size may also be influenced directly by copulation rates (Birkhead *et al.* 1993). There is some empirical evidence in support of each of these patterns, though rigorous analyses are still needed, controlling for potentially confounding variables.

While all of this is quite convincing, the other hypotheses listed here might well apply to some species either in concert with the advantages of frequent copulations in the face of sperm competition, or alone. For example, this hypothesis cannot explain the apparently low copulation rate in the American redstart, where rates of extrapair paternity are high (Sherry and Holmes 1997) and testis size is above average for a bird of its body mass (Pitcher *et al.* 2005). Clearly there are some anomalies to the general pattern that deserve further study.

H5 Male infertility. If sperm viability rates are low or males have difficulty transferring sperm during coitus, then frequent copulations would be favored (Torok *et al.* 2003). For example, particularly young and/or inexperienced males as well as old, injured or unhealthy males may suffer either low sperm viability or have difficulty copulating successfully. To the best of our knowledge, no studies have looked for either of these patterns, nor have they

been shown to influence copulation rates. The male fertility argument has been proposed to explain extrapair copulations in birds, but a comparative study of 58 bird species and a wide range of apparent infertility (0-39% of eggs) found no evidence to test this hypothesis (Morrow *et al.* 2002).

H6 Runaway selection (correlated response to selection). If we assume that hormonal changes provide the cue for male copulation behavior, it is possible that frequent copulations are simply an incidental, nonadaptive byproduct of selection for changes in hormone levels for other purposes, like aggression. Such high copulation rates would persist if the benefits from these other behaviors did not exceed the costs (e.g., higher predation risks when copulating, sperm production, energetic costs of copulation, sexually transmitted diseases, etc.). This hypothesis has not previously been suggested but may help to explain the high copulation rates of some Falconiformes in particular, where aggression over territories and mates may be high, predation risks may be low, and the energetic costs of copulating and sperm production may also be low. In this family, the large number of copulations per clutch is often spread over a relatively long period. In the Northern goshawk (*Accipiter nisus*), for example, pairs copulate up to 500 times per clutch, but usually less than once an hour during daylight hours (Rutz 2005).

6.3.4.2 Extrapair copulations

Since the advent of DNA profiling in the 1980s, it has become clear that at least some individuals in most bird species engage in extrapair copulations (Griffith *et al.* 2002; Westneat and Stewart 2003; Volume 6A, Chapter 8). These often differ from within-pair copulations in their duration, their diel and seasonal timing, their frequency and in the behavior of one or both sexes. Extrapair copulations (EPCs) can be sought by males and/or females, and sometimes forced aggressively by males (Westneat and Stewart 2003). EPCs can also be either more or less likely to result in fertilizations than within-pair copulations, though there is more evidence of the former than the latter (Westneat and Stewart 2003). In this section, we deal briefly with some of the differences between EPCs and the within-pair copulations described above, and we refer the reader to the many reviews of this topic for more details (Griffith *et al.* 2002; Westneat and Stewart 2003; Volume 6A, Chapter 8). There has been much interest in EPCs in birds because so many species were long thought to be both socially and sexually monogamous, and more recently because the patterns in EPC rates both within and between species has defied general explanation (Griffith *et al.* 2002; Westneat and Stewart 2003; Volume 6A, Chapter 8).

Forced EPCs, by their very nature, tend to be much more aggressive than both unforced EPCs and within-pair copulations, as exemplified by observations of the New Zealand stitchbird, described above. Also, forced EPCs are not usually preceded by any male precopulatory display, and seem to be surprisingly successful at achieving fertilizations, even in species without an intromittent organ. Because forced copulations do not apparently

need to involve female cooperation, they are relatively easy to explain as a male tactic for increasing his reproductive success and should be expected whenever there is (i) opportunity, (ii) a cost to females, and (iii) no net cost to males. Costs to both sexes might accrue from physical injury or sexually transmitted diseases, but females could also suffer an additional cost in the loss of paternal care from her social mate, or a reduction in the mean genetic quality of her offspring. Opportunities for extrapair copulations arise when females forage off their territories, as in the Tree swallow (Petersen *et al.* 2001), or are otherwise left ungarded by their social mate.

Several studies have found that EPCs tend to occur more often close to the time of female fertility than within-pair copulations (Fig. 6.21A,B) and usually at a lower rate (Griffith *et al.* 2002; Westneat and Stewart 2003), for obvious reasons. For example, in the Lesser kestrel, EPCs were attempted by males on paired females only during the female's fertile period and never more than 20 d before egg-laying began, whereas within-pair copulations were quite common up to 120 d before egg-laying (Fig. 6.21B; Negro *et al.* 1992). Such a bias in timing might be expected when unforced EPCs are under female control, because females should be most aware of their egg-laying period, and should be expected to be timed when last male sperm precedence will favor fertilization by the preferred sire.

6.3.4.3 Postcopulatory displays

In many birds, unforced copulations within pairs are followed by some sort of postcopulatory display, including songs and calls, and often containing elements of the precopulatory displays. Thus, in the male Common goldeneye, for example, successful copulations are followed by the 'Steaming Display' (Fig. 6.17M) which is performed while swimming away from the female, and is followed by a bout of vigorous preening and bathing (Eadie *et al.* 1995).

Some sort of ritualized postcopulatory display like this is very common in several, but certainly not all, non-passerine families (e.g., ducks, geese and swans, grebes, hawks and falcons, terns, pelicans, boobies), but is rarely observed in passerine birds. In those passerines where postcopulatory displays have been recorded, they usually consist of brief wing-quivering, preening and soft calls (Fig. 6.17F), but, in most species, no postcopulatory displays have been recorded despite intensive observational study. Postcopulatory displays are enigmatic because they serve no obvious function, nor has their function been studied in any detail. Although Austin and Miller (1995) suggested that postcopulatory displays in the Northern pintail (*Anas acuta*) might function to aid in retraction of the intromittent organ (IO), this seems highly unlikely as (i) ritualized displays should not be functionally necessary for this, (ii) females also perform these displays, and (iii) postcopulatory displays are by no means restricted to taxa in which males have IOs.

Here, we suggest three possibilities that might provide useful focus for future work. First, these displays may signal nothing at all but simply be a

byproduct of heightened sexual arousal. This seems unlikely because they rarely follow forced copulations and are sometimes absent after both within and extrapair copulations. It also seems to us that all forms of copulation should involve sexual arousal that would stimulate such displays, but postcopulatory displays seem not to occur in the majority of bird species.

Second, they might provide some sort of information about the success of the within-pair copulation, indicating to one or both pair members that the displaying sex perceived that sperm was successfully transferred during the preceding copulation. This hypothesis could potentially explain the occasional absence of such displays after a copulation attempt, and would predict that subsequent copulation attempts should soon follow. Experimental studies of captive birds might be able to detect whether sperm transfer and postcopulatory displays are associated.

Finally, these displays may reveal another kind of quality indicator. After the effort of copulating, such displays could potentially be an honest signal of male quality that could influence female sperm storage, or her willingness to copulate again with that male. Studies of captive birds might be used to manipulate the presence and/or quality of postcopulatory displays and measure the consequences of experimental manipulation.

6.4 SYNTHESIS

Over the past 40 years or so, our understanding of the reasons for variation in the courtship and copulation behavior of birds has been richly informed by a focus on sexual selection. As a result, we can now account for some of the extensive variation in the frequency and temporal patterns of copulations in birds, and the focus on courtship has shifted away from ritualized differences among species to an attempt to understand variation among individuals in the context of quality advertisement (Chapter 5). Sperm competition theory, in particular, has contributed much to the development of ideas about how all of this variation might be adaptive.

Despite the considerable progress that has been made, and the trove of interesting ideas that has been generated and formulated as testable hypotheses, we still cannot account for much of the variation that has been documented so far with respect to courtship and copulation behavior. Indeed, two of the real advantages of the recent focus on sexual selection have been to generate testable alternative hypotheses and to encourage the study of the mechanisms that underlie the observed patterns, particularly in the context of sperm competition. Thus, as we have outlined in this review, some early ideas about the influence of history, genetics and physiology on mating behaviors, outside the context of sexual selection, may now deserve some further attention. Ironically, the attention given to sexual selection may be especially useful in helping us to understand how these other factors have shaped courtship and copulation behavior in birds.

6.5 ACKNOWLEDGMENTS

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Sexual Conflict and its Implications for Fitness

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7.1 INTRODUCTION

Nick Davies' classic (1992) monograph on Dunnock *Prunella modularis* behavior and social evolution opens with a quote from *A History of British Birds* by the Reverend F. O. Morris (1856), which lauds the dunnock as "...humble and homely in its deportment and habits...", and suggests that "...the dunnock exhibits a pattern [of behavior] which many of a higher grade might imitate, with advantage to themselves and benefit to others through an improved example." Davies (1992) wryly notes that, given what is now known about the 'bizarre sexual behavior' and highly variable mating system of the dunnock, "...had his congregation followed suit, there would have been chaos in the parish...", and instead concluded that the dunnock's behavior and life history were a reflection of the various outcomes of conflicts of interest among males and females. Such sexual conflict is now considered ubiquitous in sexually reproducing taxa (Arnqvist and Rowe 2005), but, despite key contributions from Trivers (1972) and Parker (1979) over 25 years ago, the study of sexual conflict has only really taken off within the last 10 years or so (Fig. 7.1).

Here, we review how this new and rapidly expanding field of study applies to birds. In Section 7.2 we define sexual conflict and examine the reasons for, and the extent of, its occurrence. Section 7.3 explores the different forms of sexual conflict, from conflicts over mating (pre-zygotic sexual conflict) to conflicts over parental investment (post-zygotic sexual conflict), and in Section 7.4 we discuss the fitness consequences of conflict among males and females.

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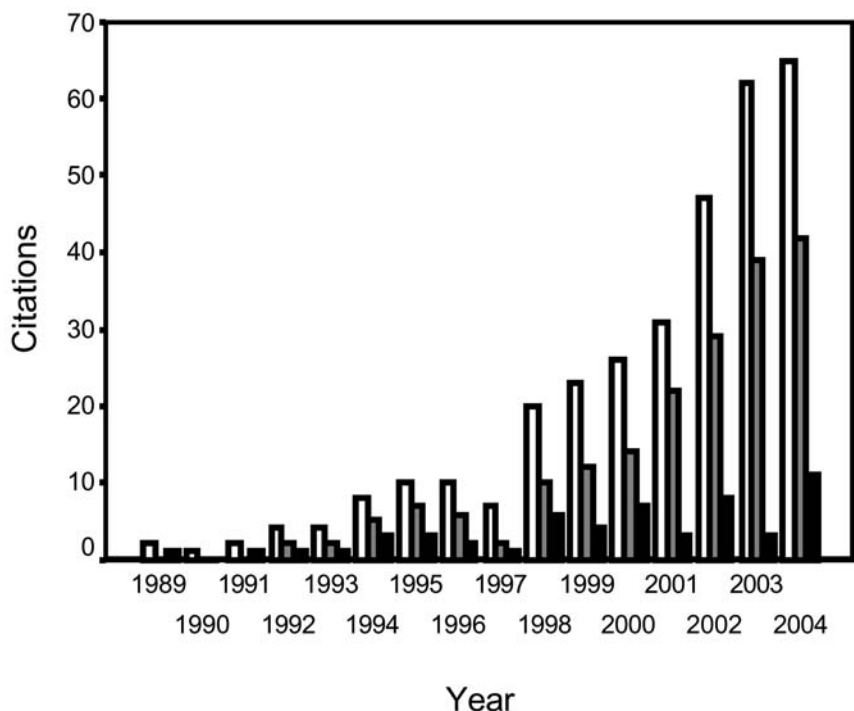


Fig. 7.1 Citations for 'sexual conflict' taken from the ISI Science Citation Index (Web of Science) for the years 1989-2004 inclusive. Unfilled bars represent total citations of 'sexual conflict', grey bars represent sub-group citations for 'mating and sexual conflict', and black bars sub-group citations for 'parental and sexual conflict'. Although papers in this latter category were not always about post-zygotic sexual conflict (for example the 3 papers in this category published in 2001 were all concerned primarily with conflicts over mating), the figure illustrates that the recent growth in the number of published papers on sexual conflict is largely a consequence of an increase in the number of papers on pre-zygotic, rather than post-zygotic, sexual conflict (see text).

7.2 WHAT IS SEXUAL CONFLICT, AND WHY DOES IT OCCUR?

7.2.1 Definitions

Conflict does not necessarily involve overt aggression. In sexual reproduction, two individuals have shared genetic interests in their offspring. If there are costs of reproduction (Williams 1966), parents will have divergent interests in the 'economics' of reproducing (Lessells 1999; Arnqvist and Rowe 2005), and additionally, sex differences in reproductive roles can result in different selection pressures for males and females, further intensifying sexual conflict. From a 'selfish gene' perspective (Dawkins 1989), evolutionary interests of individuals diverge because they do not share the same alleles for all loci, and

this creates competition among different alleles at a locus (Arnqvist and Rowe 2005). When two unrelated individuals reproduce sexually, the conflict is heightened, such that "...each parent's fitness is generally maximised if it invests less, and the other invests more, than would maximize the other parent's fitness" (Trivers 1972).

Sexual conflict can occur over any form of reproductive investment. Given this and also that the research field is relatively young, it is perhaps not surprising that sexual conflict has been defined in numerous ways. Definitions listed in Arnqvist and Rowe (2005) vary from the relatively simple, such as: 'A conflict between the evolutionary interests of individuals of the two sexes' (Parker 1979), 'When the genetic interests of males and females diverge' (Chapman *et al.* 2003) and 'Different evolutionary interests of the two sexes' (Parker and Partridge 1998), to the more complex; 'when the slope of any relation between either 1) a single trait expressed in both sexes, or 2) an outcome of male-female interactions on one hand, and fitness on the other, differ in sign in the two sexes' (Gavrilets *et al.* 2001) and the precise; 'Sex difference in the covariance between promiscuity and offspring numbers' (Shuster and Wade 2003). This variation in how sexual conflict is defined also reflects the different approaches and level of analysis of sexual conflict (Arnqvist and Rowe 2005).

At the genetic level, conflict between the sexes can occur through two distinct routes (Chapman and Partridge 1996); within a locus and between loci.

7.2.1.1 Intra-locus conflict

Intra-locus conflict occurs when the fitness optima for a given trait that is expressed in both sexes are different in males and females (Chapman *et al.* 2003). A gene expressed in both sexes can be beneficial to one sex, but detrimental to the other ('sexually antagonistic genes'; Rice 1984; Lessells 1999), leading to a genetic correlation between males and females, such that each sex impedes the adaptive evolution of the other (Chapman *et al.* 2003).

Studies of the interactions between genotype and sex, for adult fitness components, provide evidence for intra-locus conflict (Chapman *et al.* 2003). Tarsus length in Collared flycatchers (*Ficedula albicollis*) is perfectly genetically correlated in males and females (Merilä *et al.* 1997), suggesting the same gene determines tarsus length for both males and females. However, selection acts on the sexes in opposing directions, with small males and large females having better survival (Merilä *et al.* 1997). Beak color in Zebra finches (*Taeniopygia guttata*) is also highly genetically correlated (Price and Burley 1993, 1994; Price 1996). Males with the reddest beaks have the highest reproductive rate, whereas females with the most strongly orange beaks have highest reproductive rate and survival. Consequently, despite directional selection in both sexes, the evolution of beak color appears static. Similarly, different selection pressures in relation to sex on beak morphology have also been documented in Serins (*Serinus serinus*) (Björkland and Senar 2001):

selection on beak depth and width was found to be stabilising in males but directional in females.

Eventually, modifier genes with sex-limited gene expression will be favored by selection (Lessells 1999), which may lead to the evolution of sexual dimorphism (Badyaev 2002; Lindenfors 2002; Chapman *et al.* 2003). Although intra-locus conflicts are potentially common (Chapman *et al.* 2003), their evolutionary significance is unclear because there is a lack of suitable empirical studies that focus on the issue (Arnqvist and Rowe 2005).

7.2.1.2 Inter-locus conflict

Inter-locus conflict occurs when selection acts on alleles at different, interacting loci in the two sexes (Parker and Partridge 1998), so that the fitness optima as a result of the interactions are different for males and females (Chapman *et al.* 2003). This results in sexually antagonistic co-evolution between interacting traits in the two sexes (Chapman *et al.* 2003; Moore and Pizzari 2005), which leads to rapid, unpredictable and directionless changes in traits over time (Parker 1979; Chapman *et al.* 2003). Any interaction between the sexes can result in inter-locus conflict, so it has important potential consequences for a large number of biological processes and phenomena, including mate choice, parental care, sexual dimorphism, social evolution and speciation (Arnqvist and Rowe 2005). This review mainly concentrates on this route of sexual conflict.

7.2.2 A Brief History of Sexual Conflict

Historically, the production and care of young has largely been viewed as a harmonious joint-venture between males and females. This was perhaps particularly so in Victorian times, when Darwin was working and writing, where a general assumption of genetic, as well as social, monogamy meant that interactions between the sexes were considered to be non-antagonistic, and an aid to natural selection (Arnqvist and Rowe 2005).

Darwin (1871) defined sexual selection as competition within one sex (usually males) for members of the opposite sex (usually females), and differential choice by members of one sex (usually females) for members of the opposite sex (usually males). However, although he believed genetic monogamy to be very much the norm, he could not see how the most competitive or attractive males could leave a greater number of offspring to inherit their superiority, unless they were polygamous (Arnqvist and Rowe 2005). This view of harmonious male-female and familial relations continued, as exemplified by the 'Lack clutch size', which assumed that selection acted to maximize the number of surviving young per brood (e.g. Lack 1954), until the work of Hamilton (1964a, b), Trivers (1972, 1974), Dawkins (1976) and Parker (e.g. Parker and Macnair 1978; Parker 1979) in particular, brought the concept of conflict in social relations during ostensibly cooperative behaviors to a wider audience. In the 1980s the development of genetic fingerprinting (Jefferies *et al.* 1985) also put paid to the notion that genetic monogamy, if not

social monogamy, was universal; in fact, genetic monogamy in birds is rare (Black 1996). Despite this, it is perhaps less accepted that interactions between males and females can lead to a decrease in population fitness (e.g. Lande 1981; Gavrillets 2000; Martin and Hosken 2003), rather than an increase (e.g. Fisher 1915; Agrawal 2001; Siller 2001), as originally assumed by Darwin (Arnqvist and Rowe 2005). The recent upsurge in interest in sexual conflict has largely been a consequence of an increase in the publication of papers focusing on pre-zygotic conflicts over mating (see Fig. 7.1). Most of these studies have been on insects, rather than birds, however (Chapman *et al.* 2003), likely reflecting the relative ease with which data can be collected on the genetics of sexual conflict using various species of Diptera and other invertebrates. This is particularly so for conflicts that occur prior to mating, for example in relation to resistance by females of males, harassment by males, and exploitation of sensory biases (Arnqvist and Rowe 2005; Section 7.3). Sexual conflict after mating is mainly concerned with sperm competition, for which a large body of the literature is on birds (see Chapter 9 and Section 7.3). However, most work on sexual conflict in birds is concerned with post-zygotic processes, i.e. parental care (see Chapters 8 and 9 and Section 7.3). This is undoubtedly related to the virtual ubiquity of parental care in birds (Clutton-Brock 1991; Chapter 9), and the ease with which various aspects of parental investment can be observed or manipulated.

7.2.3 Origin and Extent of Sexual Conflict

Females tend to have higher pre-mating reproductive investment, primarily because of their larger gamete size compared to males (Bateman 1948; Trivers 1972). However the smaller gamete size of males means they typically have higher potential reproductive rates (Baylis 1978, 1981), which leads to a male biased operational sex-ratio and intense male-male competition (Parker and Simmons 1996). Sex differences in pre-zygotic investment leads to sex differences in post-zygotic investment.

7.2.3.1 Who cares?

Biparental care is by far the most common form of parental care in birds, occurring in over 90% of avian species (Clutton-Brock 1991; Chapter 9). But even when there is biparental care, females, rather than males, tend to provide the greater share of the care received by their young. Additionally, in species with uniparental care, it is usually the female which provides it. Why then do females care more than males? The average fitness of males and females is equal, at least in populations where the sex ratio is at parity (Trivers 1972; Wade and Shuster 2002). A bias in the amount of parental care provided by females is not expected, despite anisogamy, if parents have identical future prospects of reproduction (Kokko and Jennions 2003). However, if one sex becomes rarer than the other, differences in potential reproductive rates (Baylis 1978, 1981) will arise and there will be sex differences in future prospects of reproduction (Queller 1997).

Large numbers of small, male gametes compete for access to a small number of large, female gametes, resulting in reduced male confidence in paternity (Queller 1997). Male-male competition and/or female choice results in an elite subset of males that have a higher reproductive rate (Kokko and Jennions 2003). This increases the variance in mating success (Bateson 1948) so that males have higher potential reproductive rates than females. Reduced male confidence in paternity, combined with the higher potential reproductive rate of males, reduces the benefits and increases the costs of paternal care (Queller 1997). Consequently, sexual selection leads to post-mating sexual differences in parental care (Wade and Schuster 2002), which feed back in a loop that affects pre-mating asymmetries in investment (Kokko and Jennions 2003). Early models of parental investment (e.g. Maynard Smith 1977) did not account for equal, average fitness of males and females (Wade and Shuster 2002), so were not self-consistent (Houston and McNamara 2002), which resulted in the conclusion that post-mating sex differences in parental care lead to sexual selection, rather than the other way round (Kokko and Jennions 2003).

Relative rates of reproduction then are critical in determining the evolution of patterns of parental care (Baylis 1978, 1981), and the extent of conflict among males and females.

7.2.3.2 From true monogamy to complete infidelity

The extent of conflict depends upon the level of common interest in both current and future breeding attempts between individuals within a pair (Lessells 1999). Conflict is most intense when there is no mutual interest in offspring in the current brood, i.e. one carer is not a biological parent. At the other extreme is 'true' or genetic monogamy, where there is no conflict (Parker 1985). With true monogamy the success of an individual is completely bound together with their partner, so that, if their partner dies they cannot re-mate. So, even if only one parent provides care, as long as there is true monogamy there will be less conflict than in situations where an individual mates with a different partner at each breeding attempt. This is because such mating behavior means that an individual does not pay a cost, in terms of reduced future prospects, from his mate's increased investment in the current brood (Lessells and Parker 1999). If an individual can replace a previous mate without a cost to its future reproductive success, then there will be as much conflict as if an individual has a different partner for each breeding attempt (Lessells 1999).

Conflict can be reduced through the imposition of a cost of re-mating (Lessells 1999). This may occur if territory loss is dependent upon the loss of a partner, or when reproductive success increases with breeding experience together, as occurs for Bewick's swans (*Cygnus columbianus bewickii*) (Scott 1988) and Cassin's auklets (*Ptychoramphus aleuticus*) (Emslie *et al.* 1992). In most species of birds, however, pair bonds tend to be relatively temporary and individuals have multiple partners, creating ample scope for sexual conflict.

7.3 FORMS OF SEXUAL CONFLICT

Sexual conflict can take several forms, and each can vary in magnitude. Pre-zygotic conflict is largely concerned with conflicts over fertilization. Post-zygotic conflict is mostly concerned with conflicts over how much effort each parent puts into caring for offspring. Although these different forms of conflict may often be distinct and have independent effects there is considerable interaction and feedback between the two.

7.3.1 Conflict over Polygyny

Although most bird species are socially monogamous, social polygamy is common; where a male or female simultaneously, or serially, has two or more partners within a breeding season. Polygyny, where the male has several females, is more common than polyandry, where one female has several males. Social polyandry is common in only 2% of all bird species, but provides us with one of the classic examples of sexual conflict over polygyny in the form of Davies' study of dunnocks (Davies 1992). Male dunnocks defend territories that overlap the home ranges of females to various degrees. Some males might overlap the ranges of two females, and so become polygynous. Others might overlap the range of only one female and so become monogamous. If a male is unable to fully defend an area occupied by a female, and is forced to share her range with another male, then the female becomes polyandrous and males establish a dominance hierarchy (alpha and beta males). Stalemates can occur, in which two males share a territory that overlaps the ranges of two females, leading to polygynandry. Here both males might either unwillingly share paternity in the broods of each female, or act as two monogamous 'pairs', depending on the synchrony of breeding.

The reproductive pay-offs for these scenarios differs for males and females. Female reproductive success is maximised by breeding in polyandrous trios where each male has mating access during the female's fertile period. In this case, there are three parents to provision each brood and females generally have larger broods than when there are fewer potential carers. For males, however, this mating combination results in low reproductive success because although clutch sizes might be slightly larger, the female shares paternity between the males (Table 7.1). Males maximise their reproductive success when they have sole access to two females in polygyny. Female dunnocks only very rarely mate outside their social breeding group, so a polygynous male generally gains all the paternity with his breeding females (Burke *et al.* 1989). Females breeding with polygynous males had lower nesting success on average because males spread their parental care efforts between two broods. Furthermore, males usually showed a distinct bias in provisioning effort to only one nest, rather than dividing their time equally between the two. Nests which were attended only by the female tended to suffer a higher partial brood loss, due to the starvation of one or more nestlings. Consequently the mean

Table 7.1 Seasonal reproductive success (young fledged), for male and female dunnocks breeding under different mating combinations (modified from Davies and Houston 1986)

	Number of young fledged	
	per female	per male
Polygyny	4.4	8.8
Monogamy	5.9	5.9
Polyandry (only alpha male mates and provisions)	4.9	Alpha 4.9 Beta 0
Polyandry (Alpha and beta males mate and provision)	8.9	Alpha 4.9 Beta 4.0
Polygynandry	4.0	Alpha 5.6 Beta 2.4

number of fledglings produced from a nest without male care was only 0.81 compared to 2.41 for nests where a male helped full-time and 3.00 where two males helped full-time under polyandry. Despite this reduced success per nest, the full paternity gains meant that polygynous males still had higher overall reproductive success than males in other mating combinations because $(0.81 + 2.41) > (3.00 \times \text{paternity share})$ (Davies 1992).

In dunnocks then, sexual conflict is primarily concerned with the number of mating partners breeding individuals have. Male fitness is maximised by having sole access to several females but this gives females their lowest reproductive success. Female fitness is maximised when two males share paternity at her nest, so that nestlings are provisioned by three parents. However, this mating combination gives the poorest fitness return for males.

The outcome of the conflict between male and female dunnocks has led to the evolution of a mixed mating system where the individual winners and losers are sometimes male, sometimes female, yet in other mating systems it seems that individuals of one sex more often appear as the winners. Polygyny in Pied flycatchers (*Ficedula hypoleuca*), has been well studied by several groups of researchers in Scandinavia. Males return from Africa in spring and set up a small territory around a nest box, where they sing to attract a female. Once a female has been attracted, mated and is laying her eggs, males will often seek further reproductive opportunities by setting up a second territory distant to the first, where he attempts to attract a second female. For European birds, such polyterritorial behavior has been recorded in 37% of the 46 species where social polygyny occurs frequently, but is regarded as regular in only six species, which includes the pied flycatcher, but also the Wood warbler (*Phylloscopus sibilatrix*), Redstart (*Phoenicurus phoenicurus*), Collared flycatcher (*Ficedula albicollis*), Tengmalm's owl (*Aegolius funereus*) and Kestrel (*Falco tinnunculus*) (Møller 1986). One interpretation of this behavior in the pied flycatcher is that the females are deceived into mating with an already paired male because they perceive the territory to be vacant of existing females and so also perceive a bachelor male (deception hypothesis; Alatalo *et al.* 1981;

Alatalo and Lundberg 1990). An alternative hypothesis suggests that females are aware of the mated status of the males but are severely constrained by time, so select males quickly because they cannot afford the high search cost required to find an unmated male (the search cost hypothesis; Stenmark *et al.* 1988). Females suffer a cost to being the secondary mate of a polygynous male because the males direct their parental care efforts towards the nest of the first female and generally abandon the second female to single parenthood. This reduces the nesting success of secondary females whose nestlings are more prone to starvation than those of the primary female, but the male's reproductive success is boosted by any extra offspring that the second female might be able to raise alone. There are clearly conflicts of interests between male and female pied flycatchers, as there is in the dunnocks, but the continuum of mating combinations is limited to monogamy and polygyny, probably due to intense male-male competition.

Polygyny may also occur when conflicts are likely to be less intense than in the circumstances outlined above, and may, for example, occur on a single territory if a female chooses to breed with an already mated male because he has a superior territory (Verner and Willson 1966; Orians 1969; Wittenberger 1979; Ptak and Lachmann 2003), or because he has heritable traits which would be beneficial to the mating success of male offspring (Weatherhead and Robertson 1979; Wittenberger 1981; Alatalo and Lundberg 1986; Wagner 1994; Weatherhead 1994). Such direct or indirect benefits could offset the cost of being the secondary female and have been used to explain the evolution of polygyny in species such as the Red-winged blackbird (*Agelaius phoeniceus*) (Weatherhead and Robertson 1979) and Bobolink (*Dolichonyx oryzivorus*) (Wittenberger 1980). A long-term study of Great reed warblers (*Acrocephalus arundinaceus*) in Sweden has shown that stochastic ecological effects may also reduce the cost of polygyny for females. In this species, the secondary female of polygynous males had similar reproductive success to the primary females despite the fact that males tended to put most of their parental care effort into one nest, usually that with the older nestlings (Bensch 1996). Female great reed warblers often have to start their breeding attempts again due to the relatively high levels of nest predation, so it is quite common for females to start the breeding season as the primary female, but to be the secondary breeder by the time the chicks are ready to hatch. This means that second females do not necessarily lose male parental care, and therefore the costs of polygyny are reduced.

In other species there seems to be rather little cost to females of breeding with a male in polygyny. In Corn buntings (*Miliaria calandra*), for example, the secondary and primary females of polygynous males, and the females of monogamous males, all have similar reproductive success and so seem to suffer rather few costs to polygyny (Hartley and Shepherd 1994, 1995). In this species the males play only a minor role in provisioning of offspring in the nest (Hartley and Shepherd 1994), and so female reproductive success is less reliant on male help than it is in species such as the Dunnock or the Pied

flycatcher. Additionally, in Corn buntings, sexual selection through female choice is thought to be very weak (Catchpole and McGregor 1985; Hartley *et al.* 1993) which suggests that females are not gaining significant indirect benefits from males. With few apparent costs or benefits to females of breeding with polygynous males, it is perhaps not surprising that the most parsimonious explanation for the distribution of females amongst males is a random settlement model (Hartley and Shepherd 1995).

In lek breeding systems male parental care is absent; males inseminate females at mating grounds called leks and are usually under extreme sexual selection through female choice (Höglund and Alatalo 1995). In lek systems the sexual conflict arises over copulation; males seek matings with all females, whereas females maximise their own fitness by mating with the best genetic male. Much of the mating success of males can be attributed to female mate choice based on plumage characteristics or display rates, but there may also be traits, driven by male-male competition, which determine success (Höglund and Alatalo 1995). A classic lekking species, which shows extreme adaptations as a result of strong sexual selection, is the Peacock *Pavo cristatus*, a species where males have an elaborate plumage 'train' which they use in displays to females. Experiments have shown that females select males for mating on the basis of the symmetry of their trains and the number of 'eye-spots' they display (Petrie *et al.* 1990; Petrie and Halliday 1994). In peacocks sexual conflict results in males having a high variance in their reproductive success because a few males gain most of the matings, while most remain unmated. Conversely, females have low variance in reproductive success because they all raise a brood and tend to agree on which males to mate with (Petrie *et al.* 1992).

7.3.2 Conflict over Parentage

Sexual conflict over parentage is rife among birds. Males of many socially monogamous species seek extra-pair copulations with females who, in turn, seek to mate outside their pair bond with males of potentially higher quality than their social partners. Selection has acted upon males so that various paternity guarding behaviors have evolved, such as closely associating with fertile females, expanding territorial space during periods of peak risk, and frequent copulation to displace sperm from competing males (reviewed in Birkhead and Møller 1992). Conflicts over parentage occur most obviously between socially paired males and females, but they could also arise between females and potential extra-pair males if forced extra-pair copulations occurs, as in some wildfowl (Burns *et al.* 1980; Gauthier 1988; Davis 2002) and other species (Adkins-Regan 1995; Burley *et al.* 1996; Pizzari and Birkhead 2000).

Extra-pair copulations have been recorded frequently within socially monogamous bird species and since the invention of genetic methods for determining paternity, it has become clear that many of the copulations result in extra-pair fertilizations and consequently extra-pair young (reviewed in Griffith *et al.* 2002; Westneat and Stewart 2003). The frequency of extra-pair

offspring in broods varies considerably between species and is covered in more depth in Chapter 9. The occurrence of extra-pair young in broods is a cause for sexual conflict because, within pairs, females increase their own fitness at a cost to their partners, which lose reproductive opportunities to extra-pair males. However, extra-pair copulations may not necessarily represent an adaptive female strategy. Instead, extra-pair copulations may be the product, rather than a cause, of dynamic sexually antagonistic co-evolution, favoring offensive adaptations by males to gain extra-pair copulations and defensive adaptations by females to prevent infidelity of their social mate (Arnqvist and Kirkpatrick 2005). Aggression between females, for example, might limit extra-pair copulation opportunities, as it does opportunities for polygyny (Breiehagen and Slagsvold 1988; Kempenaers 1994; Slagsvold *et al.* 1999).

Conflict over parentage need not only involve extra-pair fertilizations. Female Wattled jacanas (*Jacana jacana*) are often polyandrous and there is a reversal in the sex roles, so that females compete for access to males, and males provide the parental care (Emlen and Wrege 2004). Female competition for access to males is intense and fights can be severe and frequent, often resulting in take-overs of males between females. Under these circumstances the winning females are often found to be taking over males that are incubating the eggs of usurped females, which creates a conflict between the sexes in that the males have paternity of the eggs, but the new females have no maternity interest in his current brood. Under these circumstances females often destroy the eggs of the previous female so that the male is free to incubate a clutch laid by the new female. Removal experiments have shown that siblicide by female wattled jacanas is directly related to this sexual conflict over parentage (Emlen *et al.* 1989).

Conflicts over parentage and polygamy are not mutually exclusive. As shown above, male dunnocks breeding as part of a polyandrous trio suffer lost reproductive opportunities compared to polygynous males (Davies 1992), however, within the polyandrous trios, there are additional conflicts over paternity. Females try to spread matings between the alpha and beta males to increase the likelihood that they will both provision the nestlings, because males only provision at nests where they have achieved mating access (Burke *et al.* 1989). Alpha males attempt to monopolise access to the fertile female, which is possible for them even when lower ranking males are present, whereas beta males try to gain exclusive access, away from the alpha male, so they can obtain matings (Davies 1992). This conflict over paternity and paternal care has led to the extraordinary mating display of cloaca pecking in the dunnock (Fig. 7.2A). Prior to copulation, males hop behind soliciting females pecking at the cloaca until the females eject any sperm they have stored inside. At that point, the males rapidly mate, and inseminate the females (Davies 1983). In ejecting the sperm of the previous male females appear to be giving the current male more confidence in his likelihood of paternity, which should increase his chances of helping to raise the brood when the eggs hatch.



Fig 7.2 **A.** Cloaca pecking in Dunnocks (*Prunella modularis*). The behavior lasts for approximately one minute prior to copulation; the male stands to the rear of the female making small pecks at her cloaca, which she displays to him with a raised tail posture. The female then dips her body and ejects a droplet of sperm stored from a previous mating, usually from another male, and then copulation takes place and lasts only a fraction of a second. Photo © Barrie Britton/naturepl.com **B.** Incubating female Kentish plover (*Charadrius alexandrinus*). There is conflict between the parents over desertion of the eggs; the parent which leaves first has a chance of increasing its reproductive success by gaining a second mate, while the other parent is left incubating a single brood. Photo: Melvin Grey.

Sexual conflict can also lead to the evolution of other extreme mating behaviors. In the Alpine accentor (*Prunella collaris*), a congener of the Dunnock, sexual conflict has led to the evolution of extremely high copulation rates. Alpine accentors breed in polygynandrous groups consisting of three or four males and a similar number of females, all of which are unrelated (Davies *et al.* 1995). Each female lays eggs in her own nest but parentage analysis, using DNA fingerprinting, has shown that paternity within broods is often mixed (Hartley *et al.* 1995). Observations of mating behavior have shown that females actively seek matings from as many males within the group as they can. This is because males will only help to provision offspring at the nests of females with which they have mated during the fertile period, so encouraging matings is a way for females to increase the likelihood of male assistance with parental care (Hartley *et al.* 1995). Males have been under intense sexual selection to maximise their chances of paternity. This has led to the evolution of large sperm storage organs, which, in combination with the females' similar willingness to mate frequently, has resulted in a very high rate of copulation; estimated at 2000 cloacal contacts per clutch (Davies *et al.* 1996). The only other passerine known to come close to this high rate is Smith's longspur (*Calcarius pictus*), which has a similar polygynandrous mating system (Briskie 1992). Females need to spread the paternity of their broods to ensure male assistance, but males maximise their fitness by having control over paternity, so, somewhat paradoxically, sexual conflict has led to the evolution of high copulation rates in alpine accentors.

7.3.3 Conflict over Parental Care

The provision of parental care is costly. This is generally considered to be based on the loss of future reproductive opportunities, either through reduced survival or because time spent providing care cannot simultaneously be used to increase other mating opportunities (parental investment; Trivers 1972; Clutton-Brock 1991). Where there are costs of parental care there will be the potential for sexual conflict.

Incubation is often taken on by the female in many species, but in others, the role is shared and provides an opportunity to see how sexual conflicts are resolved. The Kentish plover (*Charadrius alexandrinus*) (Fig. 7.2B) is a wading bird with variable incubation patterns; sometimes the eggs are incubated by either parent alone, whereas in other circumstances they share the role (Székely *et al.* 1999). Sequential polygyny and polyandry both occur in Kentish plovers and breeders that desert their current brood frequently gain a second breeding partner, while leaving their first mate to look after the eggs (Székely and Williams 1995). There is a clear conflict between the sexes when a parent has the opportunity to desert; one parent gets an opportunity to have two broods, while the other parent is left incubating a single brood. In an experimental study carried out in Turkey, it was found that the opportunity for re-mating was higher for females than it was for males; females re-mated in a median of 5.3 days compared to 25.4 days for males (Székely *et al.* 1999).

It was suggested that the difference in re-mating time was largely due to a skewed operational sex ratio (Emlen and Oring 1977), with more males being available than females. This further suggests that the benefits of desertion are much higher for females than for males, which might help explain why polyandry is so common in shorebirds like the Kentish plover, relative to other bird groups. An alternative possibility is that the birds desert the brood to reduce survival costs, but the evidence suggests that deserting female Kentish plovers do not have higher survival than females which remain with their clutches (Székely and Williams 1995).

The effect of desertion on the chicks was also examined and although in some cases the chicks raised by a single parent survived less well than those raised by two, there were equally large effects between study sites and over the course of the breeding season, suggesting that two parents are not crucial to survival (Székely and Cuthill 1999). The chicks of Kentish plovers are precocial and can feed themselves from hatching, so are only dependent on the parents for defense and shelter. Two parents are likely to be better at defending a brood than one (Fraga and Amat 1996), but the risk of predation is likely to be stochastic. As with great reed warblers (Bensch 1996), costs and benefits of sexual conflict are apparently context-dependent for Kentish plovers.

Sexual conflict over desertion also occurs in species where the young are fully dependant on the parents for food (i.e. altricial or semi-altricial species). Desertion by either sex is common in the Snail kite (*Rostrhamus sociabilis*), once the young reach the stage where they no longer need to be brooded for warmth (Beissinger and Snyder 1987). Females are twice as likely to desert than are males, with the main benefit of desertion primarily an increased opportunity for further breeding attempts. The remaining parent is usually able to rear the brood successfully (Beissinger 1990) but is likely to incur substantial costs of parental care.

Sexual conflict over desertion can even be found in species where parental provision of both food and warmth are essential to nestling survival. The Penduline tit (*Remiz pendulinus*) is a small Eurasian passerine which has uniparental care that, unusually, can be provided by either the male or female parent. Either sex can desert the other during incubation and indeed the rush to desert can sometimes lead to the nest being abandoned by both parents (female desertion, 18%; male desertion 48%; both desert 34%; Persson and Öhrström 1989). It is thought that the large, well insulated nest, that hangs safely from a branch, allows the potential for uniparental incubation (Hoi *et al.* 1996); eggs cool slowly and this gives even single parents time to forage during incubation (Szentirmai *et al.* 2005). Even when both sexes are able to desert, as in the Penduline tit, females are still at a disadvantage because internal fertilization of eggs means that they have to attend the nest until the last egg is laid, whereas males could desert as soon as it is fertilized; usually 24 hours before laying. In fact, Penduline tit males will often desert as soon as the first egg is laid, but females have evolved behaviors to counteract male

desertion. During laying, females cover their eggs and behave aggressively towards males around the nest during the laying period (Valera *et al.* 1997). These behaviors reduce the ability of males to detect when laying has started, and increase the females' chances of successfully deserting first. Only females that cover their eggs desert before their males, and experimental removal of males during laying induces females to stop the covering behavior, strongly suggesting that it has evolved in direct response to male desertion risk (Valera *et al.* 1997).

Most game theory models of desertion assume that parents behave independently, rather than in direct response to one another (e.g. Maynard Smith 1977; Houston and Davies 1985; Webb *et al.* 1999). The empirical evidence, however, suggests that desertion is contingent on the behavior of the other individual in the breeding relationship (McNamara *et al.* 2002; Griggio *et al.* 2005); if one parent deserts first, the other is left 'holding the baby' in what Trivers (1972) termed a 'cruel bind'. Although more data are needed, mainly because desertion by both sexes is relatively scarce, it is likely that desertion in birds is mostly determined by reproductive opportunities elsewhere. In the Snail kite, Penduline tit and Kentish plover, desertions are higher in the sex that is most likely to have more mating opportunities (Beissinger and Snyder 1987; Székely and Cuthill 1999). Evidence from observations of polygynandrous matings in Alpine accentors suggest that when males are faced with these options simultaneously they seek matings rather than provide parental care (Davies *et al.* 1995, 1996; Hartley *et al.* 1995). Sexual conflict over desertion is, therefore, likely to depend on mating opportunities (Magrath and Komdeur 2003) as well as the relative costs of care, and so is likely to vary with factors that influence mating opportunities, such as timing of breeding, population density, operational sex ratios, food availability and predation risk.

The outcome of sexual conflict over parental care is not usually desertion, as evidenced by the observation that most bird species show biparental care (Lack 1968). The costs and benefits of reducing parental care effort are, however, likely to be similar to those for full desertion. Experiments where males were removed during breeding have shown that although lone females can raise at least some of their offspring alone, they cannot provide enough resources to make up for the males absence and so suffer reduced reproductive success (Bart and Tornes 1989). More subtle experiments, which stimulated a reduction in parental effort in European starlings (*Sturnus vulgaris*) by adding small weights to the parents, demonstrated that a decrease in parental care by one parent was met by an increase in the workload of the other parent, but not enough to make up the total shortfall in parental care (Wright and Cuthill 1989). Together with the removal experiments, these results suggest that birds whose partners reduce parental care can suffer increased costs of the extra work, in addition to reduced reproductive success. The lower number of offspring produced per breeding attempt might be traded-off against extra mating opportunities, as occurs in polygynously breeding male pied

flycatchers (Alatalo *et al.* 1981), or Great reed warblers (Bensch 1996), but the large number of interacting variables involved make it difficult to predict the outcome of such trade-offs (Houston *et al.* 2005). Models of sexual conflict over levels of parental care need to incorporate the behavioral interactions that so obviously occur between parents (e.g. Wright and Cuthill 1989), yet many do not (reviewed in Houston *et al.* 2005). In reality, parental care decisions are most likely to be based on negotiation between parents, rather than inflexible 'sealed bid' levels of investment by individuals, which are independent of the behavior of their partner (McNamara *et al.* 1999; but see Schwagmeyer *et al.* 2002), and are likely to be context-dependent with respect to both brood hunger and parental state (Johnstone and Hinde 2006).

The original negotiation model by McNamara *et al.* (1999), which tracks the evolution of the rules that individuals might follow when faced with a drop in effort by the partner, suggests that each parent should not compensate fully, but should hold back some of their parental effort in response to the sexual conflict over workload. One prediction of this model is that offspring should suffer costs of the sexual conflict between parents so that, in some circumstances, single parents may provide more parental care than two parents together. Royle *et al.* (2002) found support for this cost to offspring of sexual conflicts in Zebra finches. Using a crossover experimental design, they showed that mothers worked harder when caring for offspring alone, and those offspring were of higher quality when raised by a single mother compared to their siblings raised by the same mother but with the help of the father. In this case, quality was expressed as the attractiveness of sons to females when they reached maturity; males raised by a single mother were preferred as sexual partners over their brothers raised by both parents (Royle *et al.* 2002). This demonstrates that the consequences of sexual conflict can be far reaching and can impact on both parents and offspring in more ways than previously expected.

7.4 CONSEQUENCES OF SEXUAL CONFLICT

Sexual conflicts are won and lost in terms of the spread of successful alleles within populations at the expense of others (Arnqvist and Rowe 2005). Although individual males and females can win or lose sexual conflicts in any given behavioral interaction, the different sexes do not win or lose at the expense of each other when the primary sex ratio is parity, because the average fitness of males and females is non-independent, and equal, as each offspring has both a mother and a father (Queller 1997; Shuster and Wade 2003; Arnqvist and Rowe 2005).

However, sexual conflict may not always be outwardly evident, due to the nature of the co-evolutionary process, where adaptation in one sex is usually matched by adaptation in the other, so there is little change in the interaction itself (Chapman and Partridge 1996). This effect is magnified by the lack of directionality of co-evolution. The resolution of sexual conflict in this context refers to this process of adaptation and counter-adaptation of the sexes, with

the dynamics of the process determined by the relative strength of selection and the relative efficacy of adaptation and counter-adaptation (Arnqvist and Rowe 2005).

This dynamism can make predictions beyond the short-term difficult (Arnqvist and Rowe 2005), but is crucial to understanding the functional significance of male antagonistic traits and female responses (Moore and Pizzari 2005). Models of interacting phenotypes and social selection provide a framework to explicitly analyse the dynamics, not just the outcome, of the co-evolutionary process (Moore and Pizzari 2005).

7.4.1 Social Selection and Indirect Genetic Effects

The effect of the social environment provided by conspecifics on genetic architecture is unusual in that the effects are both environmental and genetic (Wolf *et al.* 1998). If there is variation in the quality of the environments provided by others, and if at least some of that variation reflects genetic differences among individuals, then there are indirect genetic effects (Wolf *et al.* 1998). In these circumstances social environments are heritable and potentially subject to selection and subsequent evolution ('social selection'; West-Eberhard 1983).

Indirect genetic effects occur whenever genes expressed in one individual affect the phenotype of another (Wolf *et al.* 1998), so any form of interaction with relatives (Lynch 1987) or unrelated individuals (Moore *et al.* 1997) can result in indirect genetic effects (Fig. 7.3). When unrelated individuals contribute environmental components to the phenotype there is no covariance between the genes inherited and the environment experienced, but there may be covariance between an individual's genes and the social environment, as individuals both experience a social environment and contribute towards it (Wolf *et al.* 1998). If, for example, an individual's level of parental investment is positively affected by the level of parental investment of its partner, and vice versa, then there will be an increase in covariance between additive genetic values for parental investment and phenotype, via a feedback loop (Wolf *et al.* 1998). So the phenotype of one sex may evolve even in the absence of additive genetic variance, through social selection acting on the opposite sex (Moore and Pizzari 2005).

Models of interacting phenotypes indicate that sexually antagonistic co-evolution is likely to lead to the evolution of multiple traits in males and females, rather than exaggeration of the same traits (Moore and Pizzari 2005). This is because when a novel female trait successfully adapts to male manipulation of the original response by females, sexual selection on the male trait and social selection on the response by females will be reduced in intensity, rather than increased. Social selection creates a runaway process in which males and females co-evolve novel traits with the effect of reducing the impact of the social environment created by the opposite sex, which means selection for traits that reduce sexual conflict are opposed (Moore and Pizzari 2005).

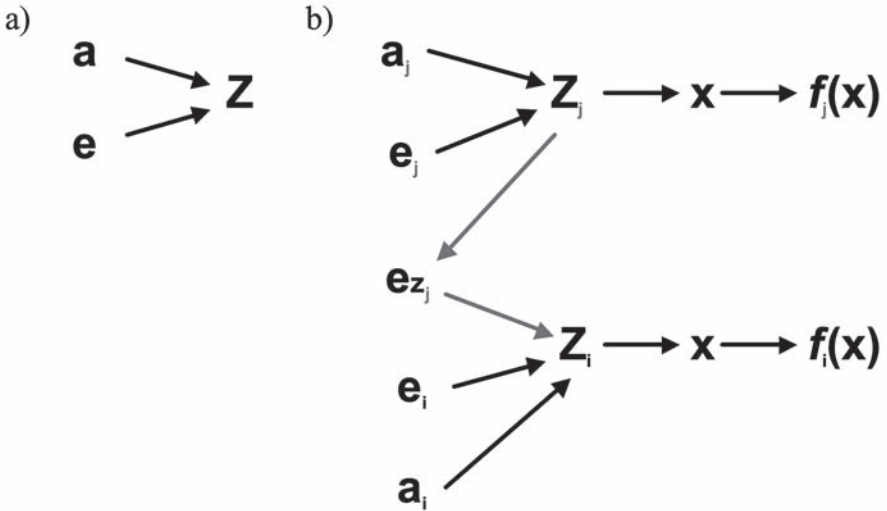


Fig. 7.3 The contribution of direct genetic, indirect genetic and environmental effects on the expression of the phenotype. a) The traditional quantitative genetic partitioning of phenotype of an individual (Z) into additive genetic (a) and environmental values (e). b) The indirect genetic effect of the phenotype of individual j (Z_j) on a second individual, i . The effect of the social environment provided by individual j (Z_j) on the expression of the phenotype of the focal individual i (Z_i) can be viewed as a heritable environmental component (ez_j) of the phenotype of the focal individual. In this schematic the social environment provided by a trait in individual j (Z_j), e.g. sexual ornaments or courtship behavior of a male, indirectly influences the mating rate (X) of individual i via trait Z_i (e.g. mating bias of females). Consequently the fitness of individual i ($f_i(X)$) is determined by Z_i directly and by Z_j indirectly through social selection. Figure derived from Wolf, J. B., Brodie, E. D., Cheverud, J. M., Moore, A. J. and Wade, M. J. 1998. Trends in Ecology and Evolution 13: 64-69, Box 2 and Moore, A. J. and Pizzari, T. 2005. The American Naturalist 165: S88-S97, Fig. 2.

Social selection has an important and complex influence on co-evolution of males and females, and in particular, emphasises the role of behavioral and phenotypic plasticity in sexual conflict (Moore and Pizzari 2005). There are, however, very few empirical studies that examine the genetic basis of variation in social environments (for an exception see Wolf 2003), despite a large body of literature that documents the importance of interacting phenotypes in parental care in influencing virtually all offspring traits (Mousseau and Fox 1998). This is particularly true where there is biparental care, which is so widespread in birds. However, a study of parent-offspring co-adaptation in Great tits (*Parus major*) by Kölliker *et al.* (2000) failed to find support for the negative covariation between offspring demand and parental supply response predicted by co-adaptation theory (Wolf and Brodie 1998; Wolf 2000), which was most likely a consequence of antagonistic co-evolution between the sexes

(Hagar and Johnstone 2003; Royle *et al.* 2004). This disruption of parent-offspring co-evolution through sexual conflict emphasises the synergistic nature of all forms of intra-familial conflict over parental investment (Parker *et al.* 2002) but also highlights the primary role of sexual conflict in the cascade of effects as a consequence of intra-familial conflict.

7.4.2 Mating Systems, Patterns of Parental Care and Mate Choice

The prospect of reduced paternal care suggests females would benefit from hiding offspring paternity (Trivers 1972). Since birds have internal fertilization there is the potential for spatial separation of males and females following copulation (Clutton-Brock and Godfray 1991), which can act to conceal offspring paternity from males. However, because male care may be compromised by additional mating opportunities (Magrath and Komdeur 2003), females spend a good deal of time attempting to limit such opportunities for males directly, or indirectly (Chapman *et al.* 2003). Direct interference in limiting male opportunities for extra pair copulations occurs in female House sparrows (*Passer domesticus*), which are highly aggressive towards other females, particularly during pair formation (Veiga 1990), as are female European starlings (Sandell 1998), which also solicit superfluous copulations to reduce their social partner's success in attracting additional mates (Eens and Pinxten 1996). Males can respond by attempting to attract additional mating opportunities away from their current home territory (e.g. Collared flycatchers, *Ficedula albicollis*; Rätti and Alatalo 1993). Female Blue tits (*Cyanistes caeruleus*) may indirectly manipulate male parental care at the expense of mating opportunities through altering the level of hatching asynchrony of the brood (Slagsvold *et al.* 1994). Experimental increases in hatching asynchrony results in increased over-winter mortality of females as females preferentially feed the smallest offspring within a brood. Conversely male mortality increases when broods hatch synchronously, as the lack of an obvious hierarchy means males contribute a greater proportion of parental investment. Females can consequently manipulate males into providing more care through a delay in the onset of incubation (Slagsvold *et al.* 1994).

Reduced parentage usually results in a drop in parental investment by males (e.g. Reed buntings, *Emberiza schoeniclus*, Dixon *et al.* 1994; Collared flycatcher, *Ficedula albicollis*, Sheldon and Ellegren 1998), but this depends upon the ability of males to assess parentage and the patterns of parentage over the lifetime of an individual (Westneat and Sargent 1996). Male dunnocks in polyandrous trios provide parental care in relation to paternity, based on access to the female during the egg-laying period (Davies 1992). On the other hand male Pukekos (*Porphyrio porphyrio*) in polyandrous trios provide similar amounts of care to one another, even though α -males sire more offspring than β -males (Jamieson *et al.* 1994). Consequently female pukekos appear to be better at concealing paternity than female dunnocks, and so get more help with parental care (Westneat and Sargent 1996). Differences in the assessment of and response to paternity may also differ between populations of the same

species, as occurs in Red-winged blackbirds (Weatherhead *et al.* 1994; Westneat 1995). Sexually antagonistic co-adaptation may therefore result in highly dynamic mating systems and suites of different behavioral adaptations.

Sexual conflict over parental investment can also favor mate choice through the advertisement of the ability to provide care (Westneat and Sargent 1996). The amount of care a male provides may depend upon the availability of alternative mating opportunities, and on underlying male quality (Westneat and Sargent 1996), which also influences both the quality of parental care and the availability of mating opportunities. Honest advertisement of parenting ability is expected when the marginal fitness returns from multiple matings are reduced (i.e. opportunities for polygamy or extra-pair copulations are limited; Kokko 1998). The effects of this can be seen in the relationship between patterns of parental care and the degree of sexual ornamentation, with extra-pair copulations favoring sexual dimorphism of structural plumage colors in birds, whereas polygyny with no male care favors sexual size dimorphism and melanin-based plumage dimorphism (Owens and Hartley 1998). When sexual conflict over parental investment is low (i.e. sex differences in parental care are minimal) the degree of sexual dimorphism is also low (Owens and Hartley 1998).

7.4.3 Life History Parameters

Comparative analyses have also been instructive in highlighting the potential importance of intra-familial conflicts in shaping life history traits in birds. The relatedness of individuals within broods of species of birds with altricial or semi-altricial young, as measured primarily by the level of extra-pair paternity, can be used as a proxy of the amount of sexual conflict.

7.4.3.1 Nestling competition

Briskie *et al.* (1994), testing predictions from models of intra-brood competition that indicate selection should favor increased competition in broods of mixed paternity (Macnair and Parker 1979; Parker and Macnair 1979), showed that nestling begging vocalizations were louder in species with lower average within-brood relatedness, suggesting that over evolutionary time birds have responded to reductions in average relatedness of nest-mates by elevating begging levels. A similar effect was found by Royle *et al.* (1999) on post-natal growth rates of young in altricial and semi-altricial species. As a result of increased competition among nest-mates, nestling growth rates are expected to be highest in those species in which siblings are less closely related to one another. As predicted there was a strong, positive association between the rate of multiple paternity and nestling growth rates, even when controlling for potentially confounding factors such as adult body size, brood size, mating system, nest predation rate and the form of parental care (Royle *et al.* 1999). Lloyd and Martin (2003) replicated this result for pre-natal, rather than post-natal, growth rates in relation to multiple paternity. The results provide

evidence to suggest that competitive interactions among related individuals within families, mediated by the effects of sexual conflict, have contributed substantially, over and above the effects of differences in proximate ecological and developmental factors between species, to the large variation in growth rates seen in the order Aves.

7.4.3.2 Clutch size

More generally, theoretical models suggest sexual conflict will lead to the co-evolution of biparental care and clutch or brood size, because the optimal clutch size from the female's point of view will depend upon the amount of care the male is expected to provide; the larger the clutch size, the more valuable the male's care (Smith and Hårdling 2000; Fig. 7.4). This result is supported by studies of sexual conflict in Zebra finches (*Taeniopygia guttata*), which have shown that parental investment is greater when sexual conflict is reduced (Royle *et al.* 2002), which has consequences for both growth rate

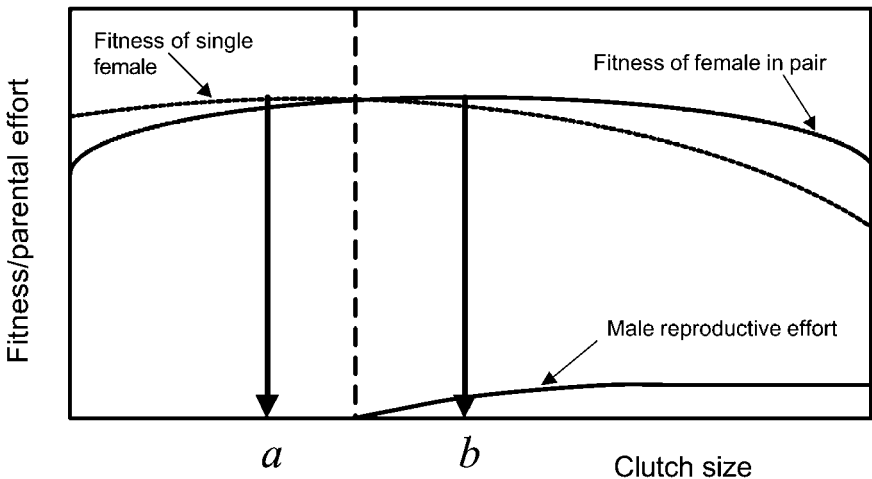


Fig 7.4. Optimum clutch sizes for single females and females in pairs when there is a threshold clutch size (illustrated by vertical dotted line). Two solutions are simultaneously stable. Below the threshold clutch size the optimum amount of care is zero, and above the threshold the male should provide some care. The fitness of single females and females in pairs is equal at the threshold value because males do not provide care in either situation. Whether uniparental or biparental care evolves depends upon the initial clutch size. If the initial size is above the threshold value biparental care and an enlarged clutch size will evolve (*b*). Conversely, if the initial clutch size is below the threshold uniparental care with a reduced clutch size will evolve (*a*). As a result, in some circumstances the social context (initial conditions) will determine the outcome of sexual conflict over relative parental investment, and hence the evolution of life-history traits such as clutch size. Redrawn from Smith, H. G. and Hårdling, R. 2000. Proceedings of the Royal Society of London, series B 267: 2163-2170, Fig. 2.

(growth rate is higher when conflict is higher, which provides within-species support for the comparative analyses of Royle *et al.* 1999; Royle *et al.* 2006) and subsequent attractiveness of offspring (Royle *et al.* 2002). Consequently the main benefit of biparental care is the increase in number, rather than the quality, of young raised (Royle *et al.* 2002, 2006).

7.4.4 Speciation

Classical population genetics theory indicates that reproductive isolation, and hence speciation, will evolve most rapidly in small, isolated populations (e.g. Lande 1981). However, because variation in reproductive traits tends to be higher than that for non-reproductive traits in closely related species, sexual conflict theory suggests that sexually antagonistic co-evolution leading to reproductive isolation will be greatest in large, allopatric populations (e.g. West-Eberhard 1983; Parker and Partridge 1998; Gavrillets 2000).

There are a number of reasons for this (Arnqvist and Rowe 2005): Firstly sexual selection involves selection on reproductive traits in both males and females. Secondly, the arbitrary nature of male-female co-evolution increases the probability of allopatric speciation, as the social environments will differ between populations (Moore and Pizzari 2005) even if there are no other environmental differences. The multidimensional nature of male signals and female resistance as a consequence of male-female phenotypic interactions also means there are a greater number of evolutionary pathways along which co-evolution can tread (Moore and Pizzari 2005). Thirdly, the non-random fusion of gametes leads to the establishment of favorable allelic combinations at different loci, meaning sexual selection is more potent at promoting subsequent reproductive isolation than natural selection (Arnqvist and Rowe 2005).

Experimental empirical support for the power of sexual conflict in reproductive isolation comes from a study using *Sepsis cynipsea* flies, which has shown that larger, denser populations with more sexual conflict diverged to a greater extent than small populations with relaxed conflict (Martin and Hosken 2003). Such large scale breeding experiments are not really feasible for vertebrates such as birds. However, comparative studies have found positive associations between rates of speciation and various indices of sexual selection (e.g. Barraclough *et al.* 1995; Mitra *et al.* 1996; Møller and Cuervo 1998; Owens *et al.* 1999), although this is not always the case. Morrow *et al.* (2003) found no relationship between species richness and testes size, as an index of post-mating sexual selection, and sexual size dimorphism and sexual dichromatism, as indices of pre-mating sexual selection across bird species. This may be because although sexual selection promotes reproductive isolation it can also increase the risk of extinction in diverging lineages through a reduction in overall fitness. If males accumulate traits that become costly to natural selection then females may also suffer from reduced fitness as a consequence, for example if mating opportunities or parental care decrease (Morrow *et al.* 2003). The net effect on species richness in any given

clade will therefore depend upon the balance between rates of speciation and extinction (Morrow *et al.* 2003).

Sexually antagonistic co-evolution is likely to be a more potent promoter of speciation than other forms of sexual selection as selection on females is exclusively direct, rather than indirect (Kokko *et al.* 2003), and females actively evade, rather than passively track, male traits, making divergence through the evolution of novelty in allopatric populations more likely (Arnqvist and Rowe 2005).

7.5 SUMMARY AND CONCLUSIONS

Sexual conflict is widespread, perhaps universal, whenever males and females interact. It arises as a consequence of differences in potential reproductive rates, operational sex ratios and intra-sexual competition between males and females, has many different forms and a multitude of consequences for a suite of patterns and processes, including mating systems, parental care, mate choice, life history traits and speciation. The key features of sexual conflict are its dynamism and lack of directionality: a consequence of the co-evolutionary process. Hence sexual conflict is a complex process with complex effects. This complexity, arising from the synergistic nature of conflicts of interest among individuals, is a layer beyond what Darwin imagined in his 'tangled bank' (Darwin 1859), but the concept is similar. Whereas Darwin viewed the complexity as interactions between species, the forms of selection operating as a result of evolutionary conflict, sexual or otherwise, also produce a rich variety and multi-layered complexity of outcomes that may be difficult to unravel.

Sexual conflict is at the heart of many important evolutionary processes and is widespread in birds, as well as many other taxa (Chapman *et al.* 2003). Individuals which gain or lose in conflicts can be of either sex, as demonstrated by the variable mating system seen in Dunnocks (Davies 1992) or the brood desertion patterns of male and female Penduline tits (Persson and Öhrström 1989) or Kentish plovers (Székely *et al.* 1999). The resolution of sexual conflict concerns the adaptations and counter-adaptations produced by the sexes as a consequence of interactions during reproduction. However, conflicts are won and lost in terms of some alleles becoming more frequent in a population than others (Arnqvist and Rowe 2005).

Despite the ubiquity of sexual conflict there is still much that we do not understand. For example, although some aspects of the dynamism involved have been incorporated (e.g. negotiation), models of conflict over parental care are too simplistic and require refining to take account of the context-dependent nature of sexual conflict. Information, or knowledge, is likely to be an important determinant of the outcome of conflict, especially where animals are involved in negotiated outcomes (Johnstone and Hinde 2006). It is rarely clear how much information individuals have of the parameters over which conflict can arise. Consequently it is important that model development is

tracked by suitable empirical work that can be used to test and amend models (and vice versa). Very little is known about intra-locus conflicts, which reflects both the lack of empirical work and the difficulties of applying in birds the sort of genetic tools used to study intra-locus conflict in insects (e.g. Chippendale *et al.* 2001). Despite that, birds remain excellent model organisms for the study of different forms of inter-locus conflict, particularly conflicts over parental care, as they show large amounts of variation within the taxa, are observable in the field, and open to experimental manipulation. Piecing together the many components which influence the levels and outcomes of sexual conflict remains a challenge for the future.

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Intra- and Extrapair Paternity

Simon C. Griffith

8.1 INTRODUCTION

The evolution of flight in birds provided an ecological advantage in terms of tracking and accessing resources and evading many predators. The almost ubiquitous use of flight in Aves, and the considerable constraints imposed by flight on structure and mass regulation are a likely cause of the highly conserved basic life-history in this class of vertebrate. Fish, reptiles, and mammals exhibit both oviparity and viviparity, but birds are exclusively oviparous and deposit their eggs in a nest, with the necessity for at least some form of parental care. The minimum requirement is incubation, whereby heat is transferred to the developing eggs directly from a parent bird. The eggs then hatch at either an altricial stage where the chicks are born completely helpless — naked, with eyes closed and are even unable to thermoregulate by themselves — or at a more advanced precocial stage where they have downy feathers and are often capable of finding food for themselves. The only group of birds in which there is no direct parental care of the young, and indeed often no contact at all between adults and young, are the megapodes. These birds place their eggs in mounds of rotting vegetation or bury them in the ground in areas where the environmental temperature is suitable for incubation (Jones *et al.* 1995). In all other avian species in which eggs or hatchlings are provided with care there is a fascinating diversity in who provides that care. In some cases care is provided by large groups of individuals cooperating together to breed, some of whom might be completely unrelated to the offspring (reviewed in Koenig and Dickinson 2004). In another extreme situation, obligate inter-specific brood parasites such as the cuckoos and cowbirds specialize in parasitizing the parental care of other species by laying their eggs in the nests of a variety of hosts (Davies 2000). Whilst cooperative breeding systems and obligate brood parasites pose some very intriguing and insightful evolutionary questions, due to the inherent conflicts of interest between the different individuals they are somewhat exceptional breeding strategies. Over 85% of species reproduce through social

monogamy, whereby a male and female form a social bond that lasts, at least through the time it takes them to fertilise the eggs, nest, incubate the eggs and raise the young to independence (Lack 1968).

The factors underlying the high incidence of social monogamy in birds have been thoroughly reviewed elsewhere (e.g. Gowaty 1996), and the evolution and maintenance of social monogamy will not be covered. However, an important general point to make is that social monogamy occurs where neither the male nor the female desert the offspring (Székely *et al.* 1996). This perspective usefully focuses attention on the direct fitness consequences of caring or desertion by the male or female. If either of them deserts, then it is likely that their offspring will suffer through lowered survival or viability leading to an immediate cost to the adults own fitness (Székely *et al.* 1996; Gowaty 1996). In those species in which social monogamy is the mating system, and in which biparental care is the system of care, individuals will generally produce more offspring by not deserting their young than by deserting them and attempting to breed polygynously or polyandrously. The male and the female remain together to raise their young simply because of the benefits to themselves in terms of offspring production.

Despite the outward appearance of cooperation between a male and female bird engaged in biparental care (Lack 1968) it soon became clear to evolutionary biologists that both individuals are selfishly pursuing their own agenda, and trying to maximize their lifetime reproductive success irrespective of that of their partner (although clearly the interests of the two will often coincide when focused on their mutual offspring). The sexual conflict that exists between the male and female is often persistent and takes a number of different forms, for example, how much care each partner will invest in the offspring (Parker 2002). The most extreme conflict between a male and female engaged in a socially monogamous bond is that concerning the paternity of the offspring. Trivers (1972) was the first to realize that in a socially monogamous mating system both males and females could potentially increase their own reproductive fitness by participating in alternative reproductive tactics that could be conducted within the constraints imposed by providing bi-parental care. Extrapair paternity (hereafter EPP) occurs where eggs are fertilized by a male other than that socially paired to the female—the putative father, and therefore obviously both females and males must indulge in extrapair copulations (hereafter EPCs) in the species in which it occurs.

When Lack (1968) classically summarized mating systems in birds it was generally thought that social monogamy reflected genetic monogamy and the incidence of EPP was unsuspected. Even after Trivers (1972) had suggested that it is likely to occur for theoretical reasons, it took many years before molecular techniques provided the tools that now allow us to routinely investigate EPP in wild birds. To date, it is my opinion that the study of EPP is still in its infancy compared to many other aspects of avian reproductive biology and I will conclude this chapter with a section on the direction that

we need to focus on to fully understand EPP. To start, however, current knowledge will be summarized, including an overview of the limitations of the data and how those data were collected.

8.2 INVESTIGATING EPP IN BIRDS

8.2.1 The Study of EPP in Birds

The study of EPP really started when Burke *et al.* (1987) used DNA fingerprinting to investigate paternity in families of House sparrow (*Passer domesticus*) collected from a colony nesting on a Nottinghamshire (UK) farm. Their study mapped the course of all subsequent studies that have followed. First came the field component where reproduction was monitored throughout the breeding season, and putative parents were identified by either catching the parents on the nest or observing them visiting the nest to incubate eggs or feed offspring. The second component focused on blood samples taken from all family members. In the molecular laboratory, DNA was extracted from this blood and analyzed using multi-locus DNA fingerprinting probes, which permitted Burke *et al.* (1987) to screen lots of random pieces of the genome and infer that when two individuals had numerous fragments of the same size then it is likely that these loci were common by descent and that they were therefore close relatives. For example if one hundred fragments were scored then we would expect a father and his genetic offspring to share approximately 50 of them on average, because the offspring gets half its genetic material from its father. Whilst undoubtedly useful, there were a number of technical problems with these methods. For example the fragments that were being analyzed were very difficult to size exactly and usually it was impossible to compare individuals that had been run on separate gels accurately, which meant that it was very difficult to search across a population to identify the fathers of extra-pair chicks. Microsatellite genotyping is now the method of choice for paternity analyses because microsatellites are codominant markers, which means that every individual has two alleles at each locus, one from its mother and one from its father allowing a more unambiguous determination of paternity and maternity because these alleles can be size scored exactly to produce a precise genotype for each individual (Queller *et al.* 1993). Regardless of the precise type of molecular analyses that has been used, these studies aim to determine whether the offspring were the true genetic products of the putative father. However, while it is relatively straightforward to establish whether a putative male actually sired a particular individual offspring, in cases where EPP does occur (the putative male is excluded as a possible father), it is often much more difficult to identify the true father. In many cases this may simply be a sampling problem because the real father may not have been captured, and therefore his blood will not have been included in the molecular analyses. More problematic, however, is that this is often a methodological problem, because molecular analyses are often not extensive enough to sufficiently

resolve differences between several possible males in the population all of whom fit as potential sires. As I will show later this general inability to identify the extrapair sire is one of the major limitations of most studies, and severely restricts our understanding.

Another major sampling issue is that studies never sample an entire population and therefore simply identifying EPP (or lack of) in a number of families, will only provide an estimate of the level of EPP in the population or species. Naturally, the reliability of these estimates are therefore very dependent on the size of the sample collected. To date, virtually all studies of EPP have very small sample sizes, with only 25% of studies sampling 200 or more offspring (Griffith *et al.* 2002). A sample of 200 offspring is the threshold at which a reasonable compromise is reached between the relative cost and effort of conducting the required behavioral and molecular analyses and further reduction in the error around the estimate (Griffith *et al.* 2002). Indeed, many of the current studies are based on less than 50 offspring (the lowest is based on just 15 individuals) and clearly such estimates are unlikely to reliably reflect the actual level of EPP. This problem is further confounded by the fact that individual chicks within a brood are not independent from one another with respect to the behavior and characteristics of the mother and father (they obviously share the same mother and putative father).

Nevertheless, despite the heterogeneity in the quality of different estimates of EPP, to date, there is a relatively impressive set of observational data on EPP in birds with over 160 studies investigating the occurrence of EPP in over 130 species. Whilst it is certainly worth being very cautious (with respect to the sampling issues discussed above) when using the estimate for the level of EPP in any two species comparison (i.e. Morton *et al.* 1998), the errors inherent in the data often tend to even themselves out over much broader comparative analyses (e.g. Arnold and Owens 2002). It is therefore perhaps not too surprising that broad comparative analyses have provided some very good insights into EPP in birds.

8.2.2 The Incidence of EPP in Birds

The application of molecular techniques has completely revolutionized our understanding of avian mating systems, such that while Lack (1968) viewed most birds as being monogamous (over 90%), today, we now believe that true genetic monogamy occurs in less than 25% of species (Griffith *et al.* 2002). While Lack (1968) divided social avian mating systems into monogamous, polyandrous, and polygynous, we are now in a position to also account for the genetic mating system. Even within socially monogamous species there exist varying degrees of genetic monogamy, polygyny and polyandry, blurring the illusion of monogamy that we get from simple behavioral studies. A recent review of the molecular studies of EPP across socially monogamous species found that, on average, 11% of offspring were sired outside the pair-bond and occurred in 18.7% of broods (Griffith *et al.* 2002).

The most important consequence of this dramatic insight of avian mating systems is the effect it has had on our understanding of sexual selection in birds. Previously, sexual selection was thought to be relatively weak in birds, because under true monogamy the variance in reproductive success amongst individuals is low, since nearly all individuals within a population get the opportunity to reproduce. However, the widespread occurrence of EPP can dramatically change the variance in reproductive success amongst individuals. From a female perspective although every female in the population cannot form a partnership with the most attractive male (because he will only have one social partner), potentially every female could copulate with him and produce offspring sired by him, which may then be fitter than those she would otherwise have had with another male. Likewise, the differences amongst males may be extreme with some males siring all the offspring in their own nest, in addition to chicks in nests of less attractive males. As a consequence, this will reduce the reproductive success of less attractive males while increasing the success of attractive males, and therefore even with a relatively low incidence of EPP in a population, the variance in reproductive success may be dramatically increased (Fig. 8.1); accounting for between 10-60% of the variance in reproductive success amongst males within socially monogamous species (Sheldon and Ellegren 1999; Whittingham and Dunn 2005).

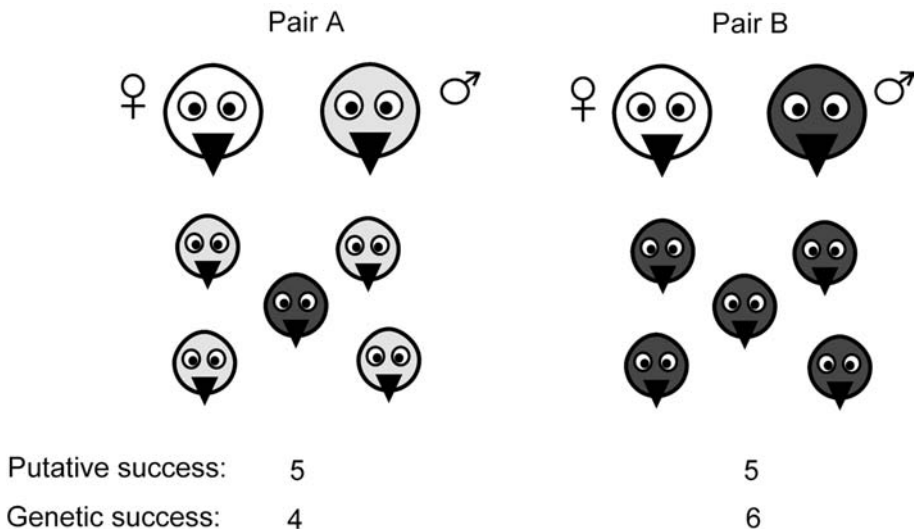


Fig. 8.1 The influence of extrapair paternity on the variance in reproductive success. The putative success of male A and male B is equal but in this example, once we use molecular techniques to identify and assign EPP we can see that in fact male B has 150% the reproductive success of male A even though brood size is quite small (5) and only one chick is fathered outside the pair-bond. Original.

In addition to revealing the almost ubiquitous nature of EPP amongst socially monogamous birds, the species that have been surveyed to date demonstrate that the level of EPP across species is highly variable. There are numerous species in which no EPP has ever been detected, despite good sample sizes and often quite clear reasons for expecting its presence (see below). For example, despite screening 122 offspring from 53 families no detectable EPP was found in the Capricorn silvereye (*Zosterops lateralis chlorocephalus*) (Robertson *et al.* 2001). At the other end of the scale, amongst socially monogamous birds with biparental care, the Reed bunting (*Emberiza schoeniclus*) has been found to have consistently high rates of EPP with over 50% of offspring detected in over 70% of broods in two separate populations in Europe (England and the Netherlands; Dixon *et al.* 1994, Bouwman *et al.* 2005). The rates of EPP are even higher in two cooperatively breeding Australian birds, the Superb fairy wren (*Malarus cyaneus*) and the Australian magpie (*Gymnorhina tibicen*) in both of which over 70% of offspring are sired by extra-group males (Mulder *et al.* 1994; Hughes *et al.* 2003). A number of studies have attempted with some success to understand the causes of this large inter-specific variation.

8.2.3 The Phylogenetic Basis of Variation in EPP

Many of the attempts to explain variation across species in the level of EPP have assumed that the rates will be dependent upon contemporary ecological factors such as breeding density and or breeding synchrony (see below). The limited success of these approaches is largely due to the fact that most of the variation in the level of EPP is deeply routed in the phylogeny, with about 60% of the variation occurring between families and orders rather than between closely related species (Arnold and Owens 2002; Bennett and Owens 2002; Griffith *et al.* 2002). This is illustrated in Figure 8.2, which uses data from Appendix 1 in Griffith *et al.* (2002) for just those families in which at least two species have been surveyed with at least 50 individuals in each species. This reveals clear consistent differences at this phylogenetic level ($r^2 = 0.56$, $F_{17, 80} = 4.71$, $n = 18$, $p < 0.0001$), to the extent that we would be reasonably confident that approximately 33% of offspring are likely to be extrapair in a randomly selected species of the Hirundinidae, whereas a member of the Passeridae is likely to have only about 7% of offspring sired outside the pair-bond. Furthermore, whilst contemporary populations of the same species may differ ecologically, when multiple populations of the same species are compared they are generally found to have very similar levels of EPP (Figure 8.3; $r = 0.76$, $n = 15$, $p = 0.001$), again underlining the fact that the level of EPP may be considered to be a species characteristic rather than something that is easily explained by contemporary ecology.

The fact that phylogeny alone accounts for such a huge component of the variation in the level of EPP across birds has a number of important implications. It suggests that like many other avian life-history traits, differences between species are likely to have been determined in the ancient

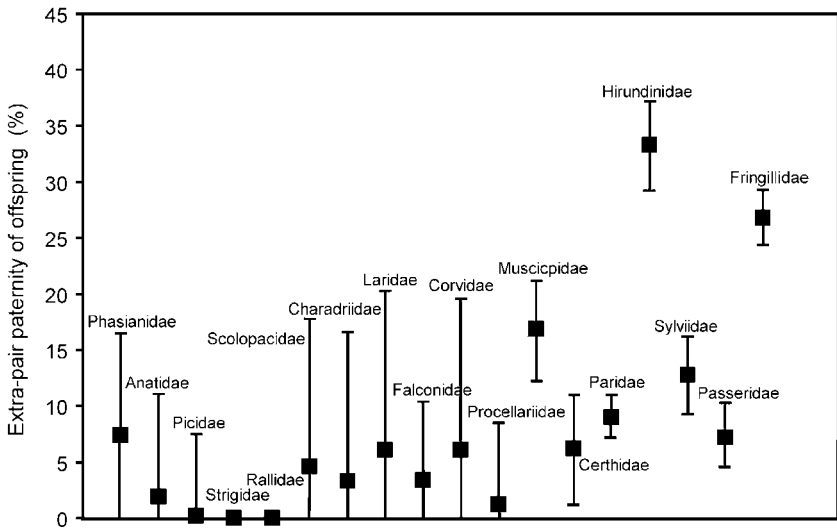


Fig. 8.2 The mean level of EPP (% offspring, $\pm$ s.e.m) across 18 avian families for which at least two species have been surveyed with a minimum of 50 offspring in each species. Original.

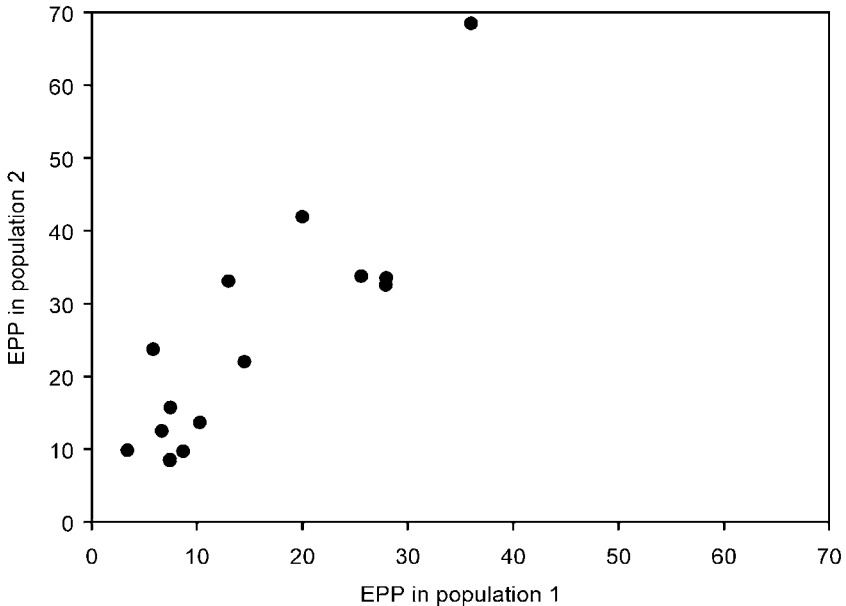


Fig. 8.3 Repeated estimates of EPP in multiply sampled species. The level of EPP (% offspring) in each of two different populations (plotted against each other) for the 15 species in which multiple populations have been sampled (using the largest two estimates if more than two populations of a species are available). Original.

evolutionary history of avian lineages (Bennett and Owens 2002; Griffith *et al.* 2002). As such, it is impossible to determine the exact selective pressures that have created the observed variation that we see today, since today's EPP levels may simply be traces of past selection in ancestral species. Alternatively of course, species within a family may exhibit similar levels of EPP because they share a very similar ecology and set of basic life-history characters, that are also phylogenetically conserved (Bennett and Owens 2002). Nonetheless, an important consequence of the strong phylogenetic determination of EPP variation is that comparative analyses must account for the phylogeny because species are certainly not independent with respect to this trait. The comparative method is a very useful first step because it will identify other traits that are correlated with variation in the level of EPP, and therefore also serve to focus further experimental work on the right kind of traits (where this is possible).

8.2.4 Ecological Correlates of the Interspecific Variation in EPP in Birds

Comparative studies have used the available data to investigate the interspecific variation in EPP with respect to a number of variables. There is a great amount of heterogeneity in the quality of these studies, both in terms of the methods they have used and the size and range of the datasets on which their analyses are based (reviewed in Griffith *et al.* 2002). Nonetheless, together, they provide the foundation for most of what we understand about EPP to date, and although I have not extensively reviewed all the relevant literature here, with respect to each variable, I will briefly summarize the best evidence for each covariate. In contrast, the study of EPP with respect to genetic variation is relatively recent and will be reviewed more comprehensively, as most of the literature has been published within the last couple of years.

8.2.4.1 The rate of adult mortality

Mauck *et al.* (1999) used state-dynamic models to theoretically demonstrate that in species in which males have a short and limited reproductive lifespan, desertion of a promiscuous female partner is not adaptive (because of limited opportunities to re-breed), and therefore higher rates of EPP should be found in these species (assuming that the benefits to females from EPP are similar across all species). As predicted (Mauck *et al.* 1999), the rate of annual adult mortality is strongly positively correlated to variation in EPP across species, explaining nearly 50% of the variation in an analysis using species as independent data points (Wink and Dyrce 1999), and about 25% when evolutionary independent contrasts were used to control for the effects of phylogeny (Arnold and Owens 2002; Bennett and Owens 2002). These studies provide strong theoretical and empirical support for a link between these two life-history traits, but of course they do not demonstrate that the relationship is causal. As yet there appears to have been no experimental support for the

relationship between EPP and mortality rates, although it is difficult to envisage an experiment that could be used to explore this correlate.

8.2.4.2 The level of paternal care

If males desert promiscuous females, withdrawing any further investment in the offspring, then in species with considerable levels of paternal care females should be less likely to indulge in extrapair copulations because they have more to lose (Mulder *et al.* 1994; Birkhead and Møller 1996; Gowaty 1996). Support for the expected negative relationship between the level of EPP and the direct effect of paternal care on reproductive success was first found in a preliminary analysis by Møller and Birkhead (1996), and has also been shown in more recent phylogenetically controlled analyses, in which about 50% of the variation in EPP rate is explained by male contribution to care (Møller 2000; Arnold and Owens 2002). In addition, Møller and Cuervo (2000) and Bennett and Owens (2002) found the same trend when considering other indices of male care (e.g. total duration of care). These comparative studies also showed that much of the variation in both traits occurred at high taxonomic levels (Arnold and Owens 2002; Bennett and Owens 2002), suggesting that ancient changes in the form of parental care may have influenced the level of female promiscuity. Again, however, these studies represent strong correlative evidence for a link between the traits, but no evidence of a causal link. In the only study which has tested the relationship experimentally, Hoi-Leitner *et al.* (1999) manipulated the abundance of food around the nest of Serin's (*Serinus serinus*) during the fertile period of female and found higher levels of EPP in areas of high food abundance. More experimental work of this nature is needed to test for a general causal link between relative food availability, the importance of paternal care to reproductive success and the level of extrapair paternity.

8.2.4.3 Breeding synchrony

Whilst measuring the overall incidence of EPP in a population it is relatively easy to acquire data on the synchrony with which a population breeds, and it is not surprising that several studies have correlated these two indices. After finding a positive correlation, Stutchbury and Morton (1995) suggested that in a synchronously breeding population females are better able to compare between males, facilitating their choice of extra-pair partners and therefore potentially increasing the benefits that may be gained from these extrapair males. Further comparative investigations have produced differing results. In their analysis, controlling for phylogeny and other confounding factors, Westneat and Sherman (1997) found no evidence for a relationship, whilst further analyses by Stutchbury (1998a,b) again found significant positive correlation between synchrony and EPP, although both were based on reduced data sets. However, if breeding synchrony does drive the variation in EPP across species then there should also be a relationship between populations within a species or across individuals within a population (Weatherhead and Yezerinac 1998). A recent review of all correlational

studies found no evidence for this relationship in ten species, a negative relationship in three species and a positive relationship in only two species (Griffith *et al.* 2002). No experiments have been conducted to date to examine the potential relationship and this is clearly an area for further work.

8.2.4.4 Breeding density

It is thought that birds breeding at high densities, and particularly in colonies, are more likely to indulge in extrapair copulations since the opportunities for finding an extrapair mate are far greater than in more dispersed-breeding species (Møller and Birkhead 1993). This idea is attractive and because it is relatively easy to estimate breeding density a number of studies have investigated the relationship. Westneat and Sherman (1997) found no evidence that interspecific variation in breeding densities affected EPP levels, although, using a greatly reduced sample size they did find a general trend within a species for high density populations to have higher rates of EPP than low density populations. However, no consistent pattern was found in a recent review of single species studies investigating the potential relationship across multiple populations; three reported positive relationships, three found no relationship and one found a significant negative effect (Griffith *et al.* 2002). An alternative approach has been taken in a number of studies that have compared the levels of EPP for different levels (e.g. families breeding at high versus low density) within a single population, finding positive relationships in four species and no relationship in a further six species (Griffith *et al.* 2002). However, a more sophisticated meta-analytical examination of the data in these studies by Møller and Ninni (1998), found a consistent positive relationship between breeding density and the level of EPP, although once more there is no evidence that the relationship is causal and some experimental work is needed.

8.2.4.5 Islands and EPP

Island populations are particularly attractive model systems for evolutionary biologists, and the investigation of EPP levels in island populations has provided no exception.. There are two main reasons why island populations might be expected to have lower levels of EPP than mainland populations. First, island populations are often genetically impoverished (Frankham 1997), and therefore the potential genetic benefits to females from extrapair males would be lower in inbred island populations. Second, islands tend to have more simple ecosystems, and such ecological constraints may select for higher levels of parental care (as above). In his comparative study, Griffith (2000a) found the predicted significant difference overall between island and mainland populations, a result which was also demonstrated by a comparison across ten species in which both a mainland and island population had been surveyed. It is clear from comparative work that there is an island effect on the rate of EPP, but there is a need for experimental work to determine whether this is driven by different ecological circumstances faced by insular populations or whether it is a product of their genetic structure (or a combination of both).

8.2.4.6 Genetic diversity

The most obvious benefits to females indulging in extrapair copulations seem likely to be indirect genetic benefits (good genes) for their offspring (see above), and therefore, the level of genetic diversity in a population will directly affect the potential benefits to promiscuous females. If the level of genetic variation is extremely low then essentially all males will be similar and a female is unlikely to gain any different genes from an extrapair male that she would from her own partner (Petrie and Lipsitch 1994). EPP should therefore be most frequent in species with high genetic diversity. Using a combination of two comparative approaches Petrie *et al.* (1998) found some support for this idea. First, in a multivariate model based on evolutionary independent contrasts (to control for phylogeny), in which the level of sexual dimorphism, sample size and body size were also included, the proportion of polymorphic allozyme loci explained 85% of the variation in the level of EPP across 35 species (Petrie *et al.* 1998). Second, in six of seven matched pairs of sister-species differing in the level of EPP, the species with a higher rate of EPP showed higher RAPD polymorphism (Petrie *et al.* 1998). Again, it must be recognised that these correlations do not demonstrate causality and it is equally plausible that the level of EPP in a population or species actually promotes the level of genetic diversity. Furthermore, the indices of genetic variation that were used (selectively neutral polymorphic markers) are far removed from 'additive genetic variation in male fitness' on which this hypothesis is based. Nevertheless, it is interesting that in their study, using the appropriate controls for phylogeny, Petrie *et al.* (1998) were able to explain a far higher proportion of the variation in EPP across species than any of the contemporary ecological variables, such as breeding density and synchrony. Furthermore, in contrast with studies on breeding synchrony where the correlative evidence across species is not supported by the same relationship within species and populations, recent studies have found that the level of genetic diversity also affects the level of EPP across families (see below).

Two hypotheses predict the relationship between levels of genetic variation and EPP, and the difference between them should be recognized when they are examined at the intraspecific level because they make slightly different predictions about which females should have EPP (Griffith *et al.* 2002). The 'genetic diversity' hypothesis suggests that females should undergo multiple mating to maximize the level of diversity amongst their brood (Williams 1975; Westneat *et al.* 1990), implicitly assuming that females are unable to determine the level of genetic similarity with their partner. By contrast, the 'genetic compatibility' hypothesis predicts that females should seek to maximize the level of compatibility between themselves and the sire of their offspring and assumes that females are capable of assessing the level of genetic compatibility with their partner (Kempnaers *et al.* 1999; Tregenza and Wedell 2000). The latter model predicts that only females that have a high level of similarity with their social partner should seek EPP, whereas the genetic diversity model suggests that all females would benefit from being promiscuous and having multiple paternity in their broods (Griffith *et al.* 2002).

Furthermore, the extrapair sires should be selected randomly with respect to their genetic make-up in the genetic diversity model, and for the level of compatibility in the second model. However, the differences predicted by these models are only important if individuals are capable of determining their level of genetic compatibility with other individuals, and thus also capable of evaluating their level of genetic similarity (which currently seems very unlikely in birds).

A number of recent studies have found a relationship between EPP in families and genetic similarity between individuals. For example some studies have found that the broods are more likely to contain extrapair offspring when the parents are more genetically similar (e.g. Blomqvist *et al.* 2002; Eimes *et al.* 2005; Richardson *et al.* 2005; Freeman-Gallant *et al.* 2003; Smith *et al.* 2005). Alternatively, one study found that extrapair offspring were more heterozygous than their within-pair half-siblings (Foerster *et al.* 2003), suggesting that the extrapair sires were genetically more compatible than the withinpair sires (although in this study the extrapair sires were not sampled). Again, all of these studies have been observational and there are no experimental tests of the relationship between genetic variation and EPP.

8.3 UNDERSTANDING EPP IN BIRDS

8.3.1 The Adaptive Function of EPP in Birds

There is little doubt that, irrespective of the ecological or phylogenetic factors which lead to EPP, when it occurs it is not distributed randomly amongst the males in a population. Young males tend to be cuckolded more often than their older counterparts (e.g. Westneat 1990), and this disadvantage in actual reproductive success is amplified by the fact that older males are more likely to sire extrapair offspring than younger males (e.g. Wetton *et al.* 1995; Richardson and Burke 1999). Similarly, attractive males are less likely to be cuckolded and more likely to gain extrapair offspring than unattractive males, whether the frequency is dependent upon the size and/or condition of the male (e.g. Yezerinac and Weatherhead 1997), the expression of his sexually selected ornaments (e.g. Sheldon and Ellegren 1999), or his song (Forstmeier *et al.* 2002). This non-random distribution of EPP amongst males in a population will consistently select for birds of good quality, often those that express the most elaborate condition-dependent ornamental traits and live longer (through the process of sexual selection). It is therefore no surprise that two comparative analyses have found strong relationships between the level of EPP and the level of sexual dichromatism, i.e. species in which the male is very colorful in comparison with a very drab female having particularly higher levels of EPP (Møller and Birkhead 1994; Owens and Hartley 1998). In addition to exerting considerable selective pressure on ornamental characters in males, EPP has also dramatically shaped male reproductive anatomy. In species with high levels of EPP females must inevitably copulate with more than one male during a single reproductive cycle, setting up strong

competition between the sperm of the two males over the fertilization of the eggs. As a consequence, species in which there is a high level of EPP, and therefore sperm competition, have much larger testes as males are selected to ejaculate large quantities of sperm in an effort to outcompete their rival (Møller and Briskie 1995). For example, in the highly promiscuous Superb fairy-wren (*Malurus cyaneus*) the testes only can account for as much as 10% of the male's body mass (Mulder and Cockburn 1993).

Extrapair paternity clearly exerts great selection pressure on males and its adaptive significance from the male perspective is obvious — being cuckolded is bad, while gaining extrapair offspring is good, because both will dramatically affect a males' overall production of offspring. The adaptive significance of EPP to females, however, is not so clear, and in fact one recent paper has even suggested that promiscuity is maladaptive in socially monogamous females and that EPCs, even in the highly promiscuous passerines, may hold no functional value to females (Arnqvist and Kirkpatrick 2005). The latter authors argue that EPCs may be the dynamic result of sexually antagonistic coevolution, with males under strong selection for offensive adaptations that increase their relative success at gaining EPCs, while females are either constrained from evolving resistance to them, or accepting them as a "best of bad job" and thus saving them from paying the costs of defense and rejecting continual advances.

The idea that EPP holds no functional value to females and results from sexually antagonistic coevolution is a fascinating idea and one that will hopefully reinvigorate a field that has been in need of a new perspective for some time. However, I personally believe that Arnqvist and Kirkpatrick's (2005) conclusion that females do not gain from EPP is perhaps a little premature as there is increasing evidence that females are willing and active participants in extrapair behavior with some good evidence that they gain both direct and indirect benefits (see below). Nevertheless, Arnqvist and Kirkpatrick (2005) highlight the fact that, as yet, we have little or no evidence for whether EPP is controlled by males or females (or a combination of both). This point was also emphasized by Westneat and Stewart (2003) who argued that too much empirical attention had been focused on females, and that future studies should consider the evolutionary interactions and conflicts that occur between all three players involved in any EPP (the female and both the within- and extra-pair male).

One of the main problems is that nearly all studies of EPP are conducted primarily in the molecular laboratory, with most incidences of EPP only detected months or even years after the event through detached studies which attempt to elucidate behavioral phenomena through molecular studies of paternity (Griffith and Montgomerie 2003; Griffith *et al.* 2004). As such, we have little or no data on the actual behaviors associated with EPP. For example, we do not know where the EPC took place, whether the female searched for, courted the extrapair sire and solicited the EPC, or whether the male intruded onto her territory, and forced the EPC. The difference between

these two scenarios is of fundamental importance to our understanding of EPP and yet both scenarios are completely compatible with all the evidence summarized above. For instance, if females were actively seeking EPP then we would expect them to find the most attractive individual in the local vicinity. Alternatively, if EPP resulted from male-male dominance interactions and females are aggressively pursued by males then we would also expect the most dominant and ornate male to sire most of the extrapair offspring. Therefore, nearly all of the present empirical work on EPP is unsuitable for distinguishing between the alternatives of female-solicited EPCs or male-forced copulations.

8.3.1.1 Female control over paternity

A number of lines of evidence suggest that females do have a large degree of control over who fertilises their eggs. First, although they have been observed in some species (e.g. the Mallard (*Anas platyrhynchos*), McKinney *et al.* 1983), forced copulations have rarely been in birds, which is most likely because it is quite difficult for a male to overpower a female (e.g. sexual size dimorphism is very slight compared to many mammals and forelimbs are unsuitable for gripping), and successfully inseminate her (due to the lack of an intromittent organ any movement by the female is likely to disrupt the cloacal contact required for successful sperm transfer). Even if an unwanted male does manage to successfully force copulation the female may still exert a large degree of control over the outcome of fertilization. In the Domestic chicken (*Gallus gallus domesticus*), Pizarri and Birkhead (2000) found that females expelled the ejaculate of subdominant males from their cloaca within seconds of an unwanted copulation. Although this form of post-copulatory control has not been observed in either other birds or in the wild, this is most likely because it would be very hard to observe, and to my knowledge no one has attempted to investigate the possibility in other species. It would certainly represent a potentially cheap and effective method through which females could reduce male control over fertilization.

In the highly polygynous lek-breeding Ruff (*Philomachus pugnax*), females also somehow exert some control over the outcome of fertilization (Thuman and Griffith 2005). Although the mechanism by which it is achieved is currently unknown, Thuman and Griffith (2005) found that in 12 of 13 families in which two males sired offspring (and in which therefore sperm competition must have occurred), the male that sired most of the offspring was less genetically similar to the female. This pattern was taken as evidence of cryptic female choice of sperm because a) there was no evidence that females were choosing to mate more frequently with males that were less genetically similar (i.e. biased behavioral pre-copulatory mate choice), and b) because the level of genetic similarity with the female is an extrinsic trait, the pattern could not have been caused by intrinsic differences between the males (Thuman and Griffith 2005). Similarly, in their experimental study of the domestic fowl (*Gallus gallus domesticus*), Birkhead *et al.* (2004) also found evidence best

explained through female cryptic choice. In their experiments they used artificial insemination to precisely control the number of sperm introduced into the female reproductive tract, thereby removing potential cues that females may use to adjust these numbers through post-copulatory behaviors (e.g. based on the female's perception of male quality; Pizzari and Birkhead 2000). They found that male reproductive success in this scenario was nontransitive and was affected by the background in which sperm competition occurred (i.e. the individual female), with individual males doing well in some contexts (females) and poorly in others.

In addition to these mechanisms of post-copulatory control, through which females could potentially influence the outcome of fertilization, even after unwanted forced copulations, it is clear that females also actively exercise pre-copulatory choice and are active participants in extrapair behavior, at least in some species. In the highly promiscuous cooperatively breeding Superb fairywren, Double and Cockburn (2000) radio-tracked females during their fertile period and found that they left their own breeding territory before dawn, flying in directly to the territory of one of the most attractive males in the vicinity, even if this meant in most cases crossing several other territories on the way. Clearly in this species the females were not simply making random forays into adjacent territories (for feeding or some other reason), and instead must have made some pre-determined choice about the male that they wished to copulate with and were extremely active in getting the copulation. Given the amount of work involved in identifying females at this early stage of reproduction (before egg-laying), capturing them and fitting a radio-transmitter, and following individuals before dawn it is not surprising that this remains the only study to have gathered such crucial data. Nonetheless, it is the best way to understand the extent to which EPCs are driven by females because we need to understand exactly what a female does throughout her whole fertile period, and whether she is an active participant in all copulations during this period. In most species even withinpair copulations are difficult to observe, perhaps because the individuals are vulnerable to predation whilst copulating and they conduct them surreptitiously. It will be even harder to observe EPCs because they are not as common, and are also likely to be more discrete because neither the male nor female will want its own social partner to see the infidelity, due to the risk of desertion or reduced parental care (Sheldon and Ellegren 1998). In total, only a handful of EPCs have been well documented in the wild (Westneat and Stewart 2003), despite the large number of researchers engaged in the study of EPP and the number of studies. The detailed behavioral study of intra- and extrapair behavior around the fertile period (following Double and Cockburn 2000) is a major priority area for future work.

In addition to detailed direct observations of females, there are other methods through which we also get a degree of insight into female extrapair behavior. For example, in their study of the Collared flycatcher (*Ficedula albicollis*), Sheldon *et al.* (1999) experimentally widowed females during their

fertile period by removing their male partner for a couple of days. It was found that females whose partners had a large forehead patch (a condition dependent sexually selected trait) were less likely to be replaced or cuckolded than those who were paired to males with small forehead patches (Sheldon *et al.* 1999). This suggests that females were deciding whether to take a new partner or seek extrapair copulations on the basis of the perceived quality of their previous partner. An alternative interpretation of these results, however, might be that other males chose not to attempt to cuckold these highly attractive males (even though they weren't actually present), in fear of the dominant status of these individuals (the forehead patch of the male flycatcher plays a key role in male dominance; Qvarnström 1997). Although this experimental male removal study by Sheldon *et al.* (1999) is one of the best amongst the very few experimental studies that have been published to date, even this study is open to alternative interpretations about whether females or males control EPP.

The majority of work on EPP is non-experimental and certainly most observations of less attractive males being cuckolded more than attractive ones could be due to male behavior rather than that of females. Most ornamental traits, whether based on color or song, have a dual function, serving to attract females as well as being involved in male dominance interactions (Griffith and Pryke 2006). Thus, the non-random distribution of paternity (lost and gained) amongst males could be explained by the outcome of competition between males for access to females, irrespective of whether they are paired or not. Subordinate, unattractive males might not be able to defend their partners from more dominant individuals seeking extra-pair copulations, and females may potentially play a completely passive role. This scenario is here considered less likely than the alternative of females actively pursuing EPCs for benefits that they can gain though, as pointed out recently, it is plausible and there is limited evidence to refute the idea (Westneat and Stewart 2003; Arnqvist and Kirkpatrick 2005).

8.3.1.2 The cost-benefit model of EPP

It is difficult to understand the adaptive function of EPP until we know whether it is something that females seek (actively) or something they are coerced into (Arnqvist and Kirkpatrick 2005). Generally, however, as pointed out by Westneat and Stewart (2003), most researchers have worked from the perspective that females actively engage in EPCs and that variation in levels of EPP across families, within a population and across species, are the result of a trade-off between the benefits they gain and the costs they suffer. Far from an exhaustive review, I will merely introduce the main direct and indirect benefits that are currently believed to influence female extrapair mating decisions.

8.3.1.3 The direct benefits of EPP

The most obvious benefit that a female gains from mating with a second male outside the pair-bond is the insurance that she gets against her partners

infertility (Wetton and Parkin 1991). If her partner's sperm is unable to fertilize her eggs then she would otherwise potentially lose her only chance at reproduction, because it will take many weeks of incubating eggs (that don't develop) before abandoning them and attempting to breed again, by which time it is likely to be too late, given the strong selection on optimal breeding time in many species. Simply by engaging in even a single extrapair copulation she maximizes the chances that her eggs will be fertilized (Wetton and Parkin 1991). Even if male infertility is very rare in the wild there will be strong selection on females to have, as insurance, an extrapair copulation, because this could mean the difference between producing offspring and complete reproductive failure. It is here considered that this is likely to be the major benefit to promiscuous females. However, there is relatively little direct empirical support for this idea, and indeed it will be difficult to address empirically. That is largely because it is difficult to measure the level of male infertility in wild birds that might be indulging in EPCs; any eggs that may have been infertile, due to a lack of fertile sperm provided by the male partner, might be fertilized instead by an extrapair male, and thus potentially infertile eggs will therefore be fertile. Furthermore, as Sheldon (1994) pointed out, if females do seek EPCs as insurance against male infertility, they are likely to consistently choose the most phenotypically attractive males, as they are likely to be more fertile and will also offer other potential benefits (see below), which will to some extent also obscure the real motive behind such a strategy. For both these reasons it will be relatively difficult to determine the extent to which females are using EPCs for fertility assurance.

By indulging in EPCs with males, whether solicited or coerced, females may also gain access to resources that may improve her current or future reproductive potential. For example, in the Red-winged blackbird (*Agelaius phoeniceus*), females solicit EPCs from males on territories adjoining the one on which they breed, and are subsequently allowed to feed on those territories, whereas those that have remained faithful to their partner are not permitted to feed on the territories of adjacent males (Gray 1997). Although to my knowledge this is the only study in which such direct benefits have been demonstrated, once again, this is probably because very few other studies have investigated them (if any others have at all). It is certainly the case that most studies that have identified the extrapair sires find a high proportion of them to be neighbouring males (Griffith *et al.* 2002), and therefore the opportunity to females for gaining these kind of direct benefits is probably high.

8.3.1.4 The indirect benefits of EPP

Largely because they have remained fashionable throughout the last fifteen years, most of the work in this field has focused on potential 'good gene' benefits that females can gain from extrapair males (reviewed in Griffith *et al.* 2002). In addition to producing a genetically diverse brood (by mating with multiple males), EPCs have traditionally been thought to be a mechanism that

females use to target specific genes for either attractiveness or viability. These benefits are indirect because they influence the fitness of the offspring, rather than the fitness of the female herself (directly). Despite the large number of studies that invoke 'good genes' benefits to explain EPP, there is surprisingly little good evidence. The fact that females seek EPCs from the most attractive males, whilst suggestive of good genes, is open to other interpretations (e.g. Sheldon 1994). The best way of obtaining unambiguous data on the genetic benefits of EPP is through the comparison of extrapair offspring with their withinpair half-siblings, and this approach has been used by remarkably few studies. For example, in the Collared flycatcher (*Ficedula albicollis*), Sheldon *et al.* (1997) found that extrapair offspring fledge in better condition than their half-siblings, with the difference being predicted by the difference in the forehead patches of their fathers. Despite this nice result, other similar studies have failed to find much evidence for strong indirect effects (reviewed in Griffith *et al.* 2002), and a recent study that used quantitative genetic models combined with meta-analytical techniques to calculate selection gradients for all the species in which extrapair offspring had been compared directly with their within-pair half siblings, found the average force of indirect selection to be only 0.004 (Arnqvist and Kirkpatrick 2005). Therefore, although only a very limited number of studies have used the correct approaches to determine the extent to which females can gain indirect benefits, currently it appears that either other benefits are more important to females, or that it does not pay females to actively pursue a mixed reproductive strategy.

8.3.1.5 The cost of EPP and promiscuity

Species form socially monogamous pair bonds because of the fitness benefits accrued from biparental care (Black 1996). Given the costs of parental investment on future fecundity and attractiveness in birds (Griffith 2000b), we would expect individuals to be very sensitive to the risk of investing substantial effort in rearing offspring sired by another individual. Therefore, the greatest cost to females (and also potentially males) who engage in extrapair behavior that is either seen, or suspected, by their partner is reduced investment in those offspring, or ultimately desertion by that individual. Either one of these is likely to impact greatly on the fitness of the offspring in that reproductive attempt (Gowaty 1996), and also on future reproduction if re-mating opportunities are limited by time or the availability of alternative partners. Many observational studies have reported the predicted correlation between the rate of EPP and the level of paternal care (e.g. Dixon *et al.* 1994), although as always, they do not demonstrate that the two things are necessarily causally linked. Once again, the best evidence for the causal nature of the relationship comes from a study of the Collared flycatcher (*Ficedula albicollis*), in which paternity was manipulated by removing the social male during the female's fertile period (Sheldon and Ellegren 1998). Males that had been separated from their partner during her fertile period responded by reducing the amount of care they provided to the offspring

(chick feeding), relative to the female (Sheldon and Ellegren 1998). This study suggests that males are under strong selection to be sensitive to the risk of cuckoldry to avoid investing maladaptively in offspring that are not their own. In many species, males have evolved strategies such as mate-guarding (following a female partner around continually during her fertile period), or copulating at high frequency with their partner in order to out compete any rival sperm in the reproductive tract (Birkhead 1987). Conversely, females have evolved a number of strategies to reduce the likelihood that any infidelity will be detected, and to reassure her partner that she has remained faithful. For example, EPCs are often conducted in a very clandestine manner, such as the pre-dawn infidelity of the Superb fairy-wren (Double and Cockburn 2000).

Despite all precautionary measures taken by females to disguise their infidelity, it is possible that only a certain proportion of females can afford to cover the costs of reduced parental care should they be detected. For example, a female on a particularly high quality territory with abundant food for rearing offspring, or a female in very good condition, is likely to be able to rear offspring on her own should her partner suspect infidelity and desert her. This is the essence of the constrained female hypothesis (Gowaty 1996), and to a large extent this may ultimately explain a large proportion of the variation in the distribution of EPP within a population.

8.4 SUMMARY AND FUTURE DIRECTIONS

The application of molecular techniques over the past 18 years has revolutionized our understanding of avian mating systems, revealing an unprecedented level of infidelity amongst socially monogamous birds, to the extent that in some families, species that are truly genetically, as well as socially, monogamous are something of an enigma. The widespread incidence of EPP in birds, the level at which it occurs in many species, and the non-random distribution of EPP amongst individuals means that EPP will make a significant contribution to the variance in reproductive success, and therefore be a major evolutionary driving force through the process of sexual selection.

Yet, despite the important role of EPP in the evolutionary biology of birds, and the large number of studies on EPP, we still do not fully understand its function, particularly to females. One of the most pressing challenges is to understand why females participate in extra-pair copulations and whether this is due to male coercion, or to the variety of direct and indirect benefits that they may gain for themselves or for their offspring. Given the importance of EPP to fully understanding avian reproductive and evolutionary biology, the extent to which observational studies out-number experimental ones is really remarkable (and worrying). It is also important that studies of EPP, which is a behaviorally driven phenomenon, need to study the behavior itself rather than simply trying to infer the behavior from post-hoc molecular studies. It is quite clear that there is much to be resolved in this area and future work, taking a more imaginative and manipulative approach, will greatly increase our

understanding of the important remaining issues concerning extrapair paternity in birds.

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Evolution of Parental Care and Cooperative Breeding

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9.1 INTRODUCTION

For many people, birds have long held special appeal. Reasons for this are several. First, most birds are diurnal and are relatively conspicuous. Second, many exhibit striking colors, intricate color patterns and complex vocalizations, all of which can be spectacularly interesting and beautiful. Third, the vast majority of birds possess a capability that many humans envy: they can fly. In addition to these factors, birds, like humans, exhibit complex social relationships, many of which revolve around parent-offspring interactions. Also like humans, the majority of avian species produce completely helpless, altricial young, which require intense parental care.

9.1.1 An Overview of Avian Parental Care

At first glance, the Class Aves appears to be quite diverse. Think of a hummingbird alongside an ostrich or an emperor penguin, for example. The fact of the matter is, however, that despite such great differences in size, proportions, and lifestyles, birds are the most homogeneous class of vertebrate animals. Nowhere is this more apparent than in the most fundamental aspects of their reproductive biology. Three facts support this assertion. First, all birds lay eggs. No other class of vertebrates is completely invariant in mode of production of young. Second, except for the social or brood parasitic species, parental care is ubiquitous. Although megapodes or moundbuilders, Family Megapodidae, are famous for their lack of post-hatch parental care, for some

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species in this group the effort expended in egg care, which is a critical aspect of parental care, is immense (Jones *et al.* 1995). Third, unlike any other vertebrate group, the vast majority of living avian species (over 90 percent) exhibit social monogamy and biparental care of eggs and/or chicks (Kendeigh 1952; Lack 1968; Ligon 1999). Thus deviations from the monogamy-biparental care syndrome are of special interest.

9.1.2 Components of Avian Parental Care

Behavioral aspects of parental care, like physiological and endocrinological aspects, can be compartmentalized chronologically. The three major components of parental care seen in nearly all birds are preparation of nests, incubation of the eggs and care of chicks. Many of these topics are closely linked to other aspects of avian breeding biology, such as mating systems. For example, incubation and care of chicks exclusively by the male ('sex-role reversal') are often tied to a polyandrous mating system, while incubation and parental care exclusively by the female is common in polygynous mating systems (Ligon 1999). As already mentioned, in the majority of non-passerine neognathous bird families, as well as in most passeriform families, social monogamy prevails (Kendeigh 1952; Lack 1968; Ligon 1999).

Oviparity and characteristics of avian and theropod (potential avian ancestors) eggs have several important ecological consequences. First, these eggs have a hard, calcium shell that provides significant protection to embryos from desiccation and attacks from microbes and invertebrates (Gill 1995). Second, the characteristic pattern of sequential laying of eggs represents the fastest way to produce large eggs and replace clutches lost to predation while at the same time reducing a female's weight for flight (Ligon 1999). Benefits to flight are probably a secondary benefit given that sequential laying is thought to have occurred in the flightless theropods possibly ancestral to birds (Varricchio *et al.* 1999; Prum 2002; but see Wesolowski 2004). Third, laying eggs in exposed nests makes it possible for both sexes to contribute equally to post-laying parental care; that is, both sexes may participate in nest building, incubation and care of the hatchlings. Moreover, in many birds the male makes major contributions to egg production by extensive feeding of its mate (Blackburn and Evans 1986; Ligon 1999).

Evolutionary patterns of postovipositional parental care are the focus of this chapter. Because the topic of avian parental care is potentially huge, due to the large number of species and the variation among birds in the major aspects of parental care, our analyses focus primarily on patterns characterizing families. Additionally we restrict our phylogenetic analyses here to parental care *sensu lato* (i.e. male-only care, female-only care, and biparental care) and make no attempt to dissect the evolutionary patterns of the individual components of postovipositional care (incubation, care of young). Instead, we review previously proposed models for the origin and evolution of avian parental care and judge the degree of support for each using information from both our phylogenetic reconstructions and from

lessons learned from other contemporary and fossil vertebrate lineages. Regardless of the ancestral parental care system in birds, the most widespread system seen today is biparental care, which as we shall see, is linked to the evolution of altriciality. In many of these altricial lineages we also see the subsequent evolution of a hyperparental care system known as cooperative breeding which we also review.

9.2 MODELS FOR THE EVOLUTION OF AVIAN PARENTAL CARE

9.2.1 Key Issues

Any attempt to explain the evolution of parental care in birds must present clear, logical arguments for the timing and ecological relevance for the evolution of several interrelated traits (Wesolowski 2004). First and foremost are issues associated with the costs and benefits to males and females under the conditions of no care, uniparental care or biparental care. These relative costs and benefits will be affected in part by the density and distribution of individuals of each sex and the associated mating system, as we shall see. Additionally, we must consider the evolution of other key traits as each relates to female fecundity, including nest type (buried versus surface), egg size and laying pattern (batch versus sequential), developmental pattern (altricial, precocial, etc.), endothermy, incubation, brooding, flight and adult growth pattern.

9.2.2 Biparental Care as the Ancestral State For Birds

Given the predominance of biparental care in most avian taxa, numerous authors have taken the position that biparental care is ancestral for birds (Lack 1968; Skutch 1976; Emlen and Oring 1977; Silver *et al.* 1985; Kavanau 1987; Clutton-Brock 1991; McKittrick 1992; Krebs and Davies 1993; Varricchio *et al.* 1999; Burley and Johnson 2002; Tullberg *et al.* 2002). However, few of these authors provide a hypothesis for how biparental care evolved either in the most basal of avian lineages or their stem reptile ancestors.

Kavanau (1987) first described a scenario in which the reptilian ancestor of birds laid eggs in batches that were subsequently covered and guarded by the parents. Parents then escorted the precocial young after the eggs hatched. With the evolution of surface nesting, parents shielded nests to prevent overheating during the hottest part of the day and covered the eggs with vegetation to reduce detection by predators when they were away. Exposure to the sun and rotting vegetation led to more rapid development. The subsequent evolution of endothermy in birds then led to the evolution of incubation behavior and double-clutching, with both sexes caring for their own clutch. Incubation allowed for the nest to be moved from open, sunny areas to more protected sites. The evolution of flight then led to selection for reduced weight in females via sequential ovulation of single eggs, with the eventual evolutionary loss of function of one ovary. Increased needs for regular incubation due to evolution of higher metabolic rates then led to the

evolution of biparental incubation at a single nest of smaller eggs, which produced more altricial young. Biparental care, to some degree, is seen at all stages of Kavanau's model.

Burley and Johnson (2002) developed a more detailed model for the evolution of biparental care in birds from maternal-only care in ancestral archosaurs. Their model is laid out in four stages. Stage one assumes that females evolved nest-guarding behavior of relatively small, batch-laid, buried eggs due to intense nest predation. They assume females had overlapping foraging home ranges and mated promiscuously with males they encountered. Males had little to gain from paternal care given low certainty of paternity due to long-term storage of sperm. This latter point, while not stated explicitly, assumes a lack of endothermy in this lineage at this point. Burley and Johnson then use basic anisogamy arguments to support the view that paternal care was prohibitively costly since it significantly reduced a male's chances to obtain additional matings (Trivers 1972).

Once female nest-guarding behavior had evolved, with a consequent reduction in rates of nest predation, females began investing in smaller clutches of larger eggs that produced precocial offspring with higher hatchling survival rates. Larger eggs coevolved with hard eggshells, which provided protection from bacteria and invertebrates and more efficient gas exchange. The subsequent evolution of surface nesting also increased gas exchange efficiency and allowed the evolution of rudimentary incubation behaviors that increased developmental rates, given the gradual evolution of endothermy. Females became increasingly selective in mate choice due to their increased investment in offspring care. Females therefore traveled widely in attempts to find high quality males, establishing the context for the familiar pattern of female-biased dispersal and male-biased operational sex ratios seen today in many birds. Females focused their attention on male traits that indicated an ability to defend high quality territories on which females established nests. At this point, males might have practiced indirect defense of nests as a byproduct of territory defense.

Stage two of the Burley-Johnson model involves the evolution of consortships between males and females. This developed initially as females remained in male territories for extended periods prior to copulation in order to judge the quality of both a male and his territory. Extensive male courtship displays and feedings may have appeared at this stage. Males gained confidence in paternity at this point, especially if endothermy reduced the likelihood of long-term storage of sperm.

Stage three is characterized by extensive biparental care as males began to help females in numerous duties at the nest. Females incorporated information on parental care skills in their assessments of male quality (courtship feedings, territory defense abilities) and became still more selective. Males began to provide care because the population was male-biased (due to higher adult female mortality as they cruise male territories) and they therefore had few options for additional matings. Evolution of male care was

gradual, since parental duties could be partitioned into small units and thus had low initial costs and high potential benefits. Males also evolved preferences for high quality females that demonstrated high fecundity and parental care abilities, leading to the evolution of monogamy. Burley and Johnson (2002) claim that the remaining avian breeding diversity can be derived from this stage of monogamy with biparental care. However, they provide no specific explanation as to how male-only care could evolve from such a state.

Stage four shows the coevolution of increased biparental care and altricial young. However, altricial nestlings require a significant increase in provisioning behavior, which would probably draw too much attention from predators for ground nesting species. Therefore, the evolution of any significant altriciality was constrained until birds evolved flight and the use of safer nest types and sites. The evolution of extreme biparental care and monogamy resulted in a more even sex ratio. Positive-assortative mating led to situations where females that were mated to low quality males began seeking extra-pair fertilizations (i.e. cryptic polygamy, Johnson and Burley 1997).

We see problems with the Burley and Johnson model. First, the model correctly incorporates the idea that the evolution of large, sequentially-laid eggs required extensive foraging effort by females. However, nowhere does it explain how females, while also providing nest-guarding behaviors, could accomplish this. Additionally, this model fails to recognize the potential costs of parental care to a female's lifetime reproductive success if adults showed a pattern of slow, continued growth as seen in most reptiles. If a female's future fecundity was correlated with body size, then females may have shown significant costs in lifetime reproductive success if they reduced foraging rates in order to care for young (Maynard Smith 1977; Ridley 1978; Shine 1988).

9.2.3 Male-only Care as the Ancestral State for Birds

Other authors hypothesize that male-only care is the ancestral condition for birds (Elzanowski 1985; Handford and Mares 1985; van Rhijn 1984,1990; Ligon 1993, 1999; Wesolowski 1994, 2004; Vehrencamp 2000). We now outline a composite model for the evolution of male-only care derived primarily from Wesolowski (1994), but also incorporating our own ideas and additional details from the other authors listed above.

The first step in the evolution of parental care in the lineage ancestral to birds involved reproductive and physiological patterns more like 'typical' reptiles. Ectothermic males defended resource-rich territories that attracted females which mated and deposited batches of eggs in nests buried in soil or vegetation. Females chose males based on territory quality due to the importance of these resources for the initial development and survival of their young after hatching. In the process of territorial defense, males provided indirect nest defense to multiple nests and hatchlings.

Females began to lay larger eggs for the development of precocial or superprecocial young in response to selection pressures associated with high rates of predation on hatchlings. These young were able to either run or

possibly fly shortly after hatching, which probably reduced post-hatching predation rates. Evolution of larger eggs was accomplished by the evolution of sequential rather than simultaneous egg production. Production of large eggs forced the evolution of surface nesting due to the physiological limitations of gas exchange across the shell surface. The first form of more directed parental care was probably simple guarding of these surface nests. Nest guarding led to significant increases in survival of these exposed, slow-growing eggs but resulted in energetic costs associated with reduced foraging.

Assuming that it only takes one parent to adequately guard a nest, which parent should provide this care? The challenge in explaining the initial evolution of male-only care is to address two related and fundamental questions. First, why would females have abandoned their heavily invested, large eggs if parental care had significant offspring survival benefits? Second, why would males have stayed with eggs and provided care when they had the opportunity to leave well before females could have completed a clutch?

The possible distribution of a female's eggs may provide one explanation for why females did not care for eggs. Females may have spread their eggs among multiple nests to spread the risk of predation (as is seen in some megapode species today (Jones *et al.* 1995; Ligon 1999)). This behavior, however, would also have made it impossible for a female to guard each nest.

There is an additional, more fundamental reason to think that females were constrained from providing initial nest-guarding duties. The ability to produce large eggs was only possible after the evolution of a sequential pattern of egg laying. Sequential laying allowed females to acquire resources for each egg as it was laid, but put a premium on a female's ability to maintain high foraging rates throughout the prolonged laying period. Nest guarding behavior would have limited the foraging ability of females and would have therefore been prohibitively costly. Additionally, parental behavior might prove especially costly to future reproductive success (Williams 1966).

Owens (2002) found no support for this idea. When considering all contemporary lineages showing male-only care, female abandonment was not correlated with the production of larger or heavier eggs and clutches in these lineages. However, male-only care may exist in different contemporary species for varying reasons. Additionally, the selective factors that maintain this behavior today may be different from those that led to the original evolution of the trait. These factors may obscure the relationship between the production of large eggs and female foraging constraints that do exist in specific lineages. Megapodes provide examples that support this linkage (reviewed in Ligon 1999). Females of the Australian brush-turkey (*Alectura lathami*) and Malleefowl (*Leipoa ocellata*) produce large (representing a large fraction of their body weight: 12% in the latter species and even higher in others), especially yolk-rich eggs that produce superprecocial young. Females of these species spend most of their daily activity foraging in order to produce additional eggs. This high rate of foraging would not be possible if they were forced to care for the incubation mound containing these slowly developing eggs (50-96 days in Malleefowl).

Given the probably prohibitive costs of parental care to egg-producing females, were there conditions in which males benefited from providing care? Male-only care could have represented a pure ESS (i.e., an evolutionary stable strategy for male parental behavior in which all alternative male behaviors would show lower fitness and therefore fail to evolve) when care had significant benefits and minimal costs (van Rhijn 1984). Males may have maintained the ability to court and copulate with additional females while guarding nests on their territories (Trivers 1972). Females may have actually chosen males whose territories already contained eggs, since individual eggs in larger egg clusters benefited from the dilution effect (Lack 1968), which also led to the evolution of laying eggs communally in preferred males' nests (Vehrencamp 2000). This advantage of male care is seen in some teleost fish (Ridley 1978; Gross and Shine 1981; Unger and Sargent 1988).

An alternate reason why males might have benefited from providing parental care relates to female density. If female densities were low, then males may have had limited options for gaining additional matings, even if they did abandon the nest to search for other mates. Male nest guarding would then have had low costs and significant benefits if males had a high probability of paternity. Males would have gained assurance of paternity if they guarded females as the latter used the resources on the males' territories during the long periods between successive eggs. If endothermy had evolved at this point, then females would also have had limited abilities for long-term sperm storage, giving males further assurance of paternity. Owens (2002) did find that in contemporary species, male-only care was associated with low nesting densities.

Once surface nests evolved, males increased effectiveness of nest guarding by covering the eggs. Incubation, especially at night, increased rates and regularity of development. This stage could have been accomplished by either endothermic species, or initially even by ectothermic species, if males covered eggs after having reached higher preferred body temperatures. Gradual evolution of incubation behavior and incubation-dependent egg physiology might have made it possible for a male initially to rotate incubation at multiple nests or some of the eggs in large clutches. Increased regularity of incubation behavior led to gradual evolution of more rapid developmental rates and obligate parental care behavior via the necessity for incubation. Egg physiology, increased developmental rate, incubation behavior and endothermy probably coevolved over a substantial time period. Predation of ground nests probably was still high; however, increased developmental rate and care of young by males reduced the selective advantage of superprecocial young, allowing selection for hatching of less well developed young (but still relatively close to the precocial end of the developmental spectrum).

As male care became more important to nest success, females began to choose mates based not only on territory quality but also on indications of male parental care abilities. High quality males attracted multiple potential mates; however, males became able to care for fewer eggs as the needs

increased for both constant rates and earlier initiation of incubation (needed before the first egg became unviable, Prum 2002). These pressures set the stage for the male to become increasingly interested in mating only with the highest quality females and providing care only when they had confidence in paternity. An extended period of courtship coupled with an extended laying period allowed males to assess female quality and increased their certainty of paternity, especially if the potential for long-term sperm storage was reduced due to endothermy.

Two mating patterns may have emerged, given these conditions. In some lineages females competed for males, which led to polyandry and reversed sexual dimorphism. In other lineages, once females began laying larger clutches of even smaller eggs into one nest, the stage was set for the coevolution of monogamy, biparental care and altricial young. Production of altricial young allowed parents to spread the cost of reproduction over a longer period by feeding less well developed hatchlings. This extended investment could then evolve into more even contributions by both sexes (Ar and Yom-Tov 1978). Females may have first begun providing care in situations in which males faced a high probability of death such that females stayed with the nest in case they were required to assume the parental role. Females would also be expected to provide regular parental care where males alone were typically unable to provide sufficient care. This was true in harsh environments, in which incubation regularity is most important, or in areas where predation pressure was especially strong and required multiple sentinels. The evolution of biparental care could also have evolved through an initial stage of double clutching, in which females laid one clutch requiring male care and a second clutch to which she provided care. If subsequent ecological conditions made the success of the second clutch unlikely or unprofitable, then the stage was set for biparental care to evolve if it resulted in significant offspring survival benefits at the first nest. A key innovation that made the evolution of altricial young possible, in addition to monogamy and biparental care, was the evolution of safer nest sites (Burley and Johnson 2002; Dial 2003), most likely cavities, either in trees or the ground.

Burley and Johnson (2002) point out several 'readily apparent' problems with the male-only care first model. First, they use the 'common equals primitive' argument as evidence for female-only care as the ancestral state in the lineage giving rise to birds. They claim that, since most extant archosaurs and other diapsids show maternal-only care (when any care is shown at all), female-only care is primitive for the ancestral lineage leading to birds. This argument does not include information from other relevant lineages (e.g. the theropods, as discussed below). Any attempt to understand patterns of trait evolution must consider the distribution of taxa and their characteristics and not rely solely on numerical superiority (e.g. Zach 1995).

Second, Burley and Johnson claim that it is highly unlikely that males would evolve the responsibilities of uniparental care due to the prohibitive cost of lost mating opportunities resulting from time-intensive nest guarding

and incubation. However, this is exactly the pattern shown by some primitive living birds, including nearly all ratites, the tinamous and some members of the galliform family Megapodidae (e.g., the Australian Brush Turkey). Many of these birds gain, rather than lose, mating opportunities as a result of nest-guarding and incubation, as females seek males that provide nests for their eggs.

In agreement with the empirical evidence based on living species, the model outlined here shows how initial nest guarding and then incubation behaviors can be adaptive for males in the context of mate acquisition. Clearly, such behaviors do not reduce a male's potential for additional matings under all ecological circumstances and they even help a male attract multiple mates in a manner analogous to those seen in many teleost fishes. Transitions from no care to male-only care are common in teleost fishes and anurans and are even seen in some arthropod lineages. The ecological factors related to these transitions include male territoriality and low cost of paternal care that is subsequently used as a sexually selected trait to attract females (Reynolds *et al.* 2002). This scenario is consistent with the model described here.

9.2.4 Lessons from the Fossil Record

The theropod lineages that are perhaps the most closely related to birds laid large, asymmetrical eggs that are thought to have been produced sequentially over a number of days (but see Wesolowski 2004 for a critique of these conclusions). Some eggs were apparently laid in pairs and clutch sizes ranged from 12-30 eggs with a minimum of 6-15 days required to produce a clutch (Varricchio *et al.* 1997; Horner 2000). There is evidence of exposed nests with portions of eggs buried in sediment. Partial burial may have been necessary to reduce movement since reptilian eggs lack a chalaza and cannot be rotated. Surface nests found thus far show no evidence of vegetation covering the eggs for camouflage or for providing heat from fermentation (Varricchio *et al.* 1997; Horner 2000).

Tight spacing of clutches and the presence of adults at nests in postures similar to those of incubating birds suggest incubation of eggs in *Oviraptor*, *Troodon* (Norell *et al.* 1995; Varricchio *et al.* 1997) and brooding of hatchlings in *Psittacosaurus* (Meng *et al.* 2004); however, there are no indications of the sex of the caring adult. The resting/sleeping posture seen in *Mei long*, another troodontid theropod, in which the body rested on folded hind appendages with the head tucked under a folded forelimb, suggests conservation of heat and endothermy (Xu and Norell 2004). The degree of ossification in *Troodon* embryos suggests that they were precocial (Varricchio *et al.* 1997).

Considering the aggregate evidence for postovipositional parental care in those theropods possibly representing the sister group to birds, the homology of parental care in non-avian reptiles and birds is reasonable (but see Wesolowski 2004 for an alternative view). Additionally, we predict that comparative physiological studies will show common proximate mechanisms (hormonal control systems) associated with parental care in crocodilian and

avian lineages, further supporting an ancient origin of parental care homology. Unambiguous determination of the sex of provisioning adults in the avian ancestor (possibly a theropod) is crucial for an accurate ancestral reconstruction, as we show in the reconstructions described below.

The parental care conditions indicated by the fossil record are consistent with predictions of male-only care first models. Females producing such large eggs would benefit most from abandonment of the clutch in their quest to gain resources to increase fecundity in one of two ways. First, significant additional resources would be required to produce additional clutches of large eggs in a breeding season or year. Alternatively, females might maximize foraging rate to invest in continuous somatic growth that might lead to increased size-dependent future fecundity as seen in some teleost fishes (Gross and Sargent 1985). Production of extra eggs or clutches is probably the relevant selective advantage for those lineages of theropods most likely ancestral to birds, since they appear to have had a much more rapid, determinant developmental pattern than 'typical' reptiles. These lineages were, therefore, unlikely to have had fecundity benefits associated with annual somatic growth (Padian *et al.* 2001). The fossil record also suggests that extended laying periods were needed to produce clutches of these large eggs. This period may have led to an extended pairbond which increased male certainty of parentage, thus increasing the likelihood of benefits to males providing parental care.

Are there post avian-origin fossils that can shed light on the parental care systems of early birds? Feduccia (1995, 1996) claims that all living neognathous birds are derived from the 'transitional shorebirds' of the late Cretaceous. Other studies have suggested that some of the oldest living shorebird lineages showed male-only care (van Rhijn 1984). Could these observations support an interpretation that male-only care in fossil and contemporary shorebird lineages is homologous? Could the 'transitional shorebirds' in turn retain this behavior from the common ancestor they shared with paleognaths whose ancestral state is also male-only care? In other words, might the male-only care systems seen in some living shorebird lineages be homologous to those seen in the paleognaths and represent the ancestral condition for all birds (Fig. 10.3 in Ligon 1999)?

Recent phylogenetic work does not support this view. Rather, it places the shorebirds well within neognathous birds (Cracraft *et al.* 2004) with biparental care as the ancestral state for shorebirds (Székely and Reynolds 1995; Reynolds *et al.* 2002). Additionally, recent mitochondrial phylogenetic work dates the origin of modern lineages well before the 'transitional shorebirds' and the KT boundary, indicating that they are unlikely to be the founding lineage of modern birds (Paton *et al.* 2002). This scenario would also require a significant number of additional evolutionary transitions between parental care systems on the trees used in this study (ranging from 51 to 56 transitions when forcing a homologous link compared to 44 transitions seen in the most parsimonious reconstructions used in this study).

9.2.5 Lessons from Fish

One particularly important characteristic of parental care is shared by fish and birds: both sexes have equal abilities to provide most forms of postovipositional care. This fact, and others detailed below, makes comparisons of these two taxa particularly instructive and may signify parallel patterns of parental care evolution.

Of the fish species in which parental care is seen, 50% show male-only care with female-only and biparental care seen in the remaining 30% and 20% of the species, respectively (Gross 2005). Patterns of development in fish predispose males to provide care when uniparental care is advantageous. Fish show a continuous pattern of growth and, as fecundity increases with body size, this puts a premium on rapid female growth. Male reproductive success is not tightly correlated with size and therefore when uniparental care is advantageous there is selection pressure on females to abandon the clutch (Gross and Sargent 1985). Males are then left to either abandon as well, or to assume the sole care of the clutch. The evolution of male-only care in this context is not surprising since parental care has minimal energetic costs in many fish (guarding nests, fanning eggs), and may not reduce the probability of future matings. Females may copy each other when choosing mates or may prefer to lay eggs in occupied nests with the result that their eggs can benefit from the dilution effect. Nest defense therefore may be an important means of increasing males' chances of gaining additional matings (Ridley 1978; Gross and Shine 1981; Unger and Sargent 1988).

9.3 PHYLOGENETIC PATTERNS

9.3.1 Ancestral Reconstructions: Previous Studies

McKittrick (1992) developed a phylogenetic tree using behavioral and hindlimb muscular characters and used this tree to reconstruct the evolution of subcomponents of postovipositional care. Her reconstructions showed biparental defense of eggs and young and fledgling care as the ancestral conditions in birds. For incubation and nestling care, female-only, biparental and no care are each seen as equally parsimonious. Vehrencamp (2000), however, concluded that male-only care was ancestral in birds in her phylogenetic analyses of incubation evolution.

Tullberg *et al.* (2002) conducted phylogenetic analyses similar to those in our study. They conclude that the most parsimonious ancestral state for birds is biparental care via maternal-only care in the lineage preceding birds. They go further to claim that this conclusion is robust to varying assumptions concerning the sister group to birds and the parental care system of that group. Re-analyses of their data using their van Tuinen (2000) tree and assuming that theropods, with different parental care systems, are sister to birds, does not support this assertion. Indeed, when alternately assuming that theropods showed no care, male-only care, female-only care or biparental care, the most parsimonious ancestral state in birds is reconstructed as

equivocal (i.e. either state equally parsimonious) for male- or biparental care in the first two situations or as biparental in the latter two situations. Therefore, the only firm conclusion that can be drawn from these data is that ancestral birds had *some form of parental care other than care solely by the female*.

9.3.2 Ancestral Reconstructions: Current Study

Our analyses are similar to those of McKittrick (1992) and Tullberg *et al.* (2002); however, we consider other ingroup and outgroup taxa and examine different tree topologies. We first consider the phylogeny of Sibley and Ahlquist (1990) with a basal split between the paleognaths and Galloanserae (van Tuinen *et al.* 2000) and then look at how modifications of this topology (our 'composite tree'), based on more recent phylogenetic work (reviewed in Cracraft *et al.* 2004), affect the robustness of our ancestral character state reconstructions. Our composite tree is derived from the general consensus phylogeny of Cracraft *et al.* (2004, Figure 27.10); additional resolution in the passerines comes from the work of Barker *et al.* (2002) and Ericson *et al.* (2002). All remaining polytomies in this composite tree were resolved arbitrarily to allow reconstruction of the parental care evolutionary patterns using ordered characters in MacClade (see below).

Our outgroup taxa include Amphibia, Mammalia, Squamata (lizards and snakes), *Sphenodon* (tuataras), Chelonia (turtles), Crocodilia and Theropoda. As will be shown, the relative positions of these outgroup taxa have a major impact on which ancestral character state for parental care is reconstructed for the lineage leading to birds. We examine four different outgroup branching patterns grouped in two basic categories and their effects on ancestral reconstructions. First, recent phylogenetic studies question the traditional placement of the turtles (Chelonia) as a basal reptilian lineage. Turtles may in fact be more derived and squamates may be more basal than previously appreciated (Lee *et al.* 2004). However, the structure of the spermatozoa of squamates appears to be highly derived relative to those of Chelonia (Jamieson 1999 and references therein). Second, the reptilian lineage most closely related to birds is still hotly debated (Feduccia 2002; Prum 2002) and we reconstruct patterns with birds sharing an immediate common ancestry with theropods and with a more basal archosaur lineage. These four outgroup patterns were examined with both the Sibley and Ahlquist tree (1990) and our composite tree for a total of eight topologies used to reconstruct patterns of parental care evolution. (In Volume 6A, Chapter 8 Jamieson argues, from spermatozoal ultrastructure, that the Crocodylia is the extant sister-group of Aves.)

Taxa are coded as having 'no care', 'male-only care', 'female-only care' or 'biparental care'. Various amphibians and squamates show some form of parental care; however, the derived positions of these lineages suggests that 'no care' is the ancestral state for these groups (Shine 1988; Lehtinen and Nussbaum 2003). No turtle species shows clear parental care behavior; however, all crocodilians show either female or biparental care. Therefore, we code this group as polymorphic (Shine 1988). Female tuataras guard their

nests against conspecifics (Shine 1988). Female care is also the probable ancestral state for mammals (Clutton-Brock 1991). Several studies indicate that the theropod lineages perhaps most closely related to birds provided some form of parental care; however, the sex of the caring adult is not known (Norell *et al.* 1995; Varricchio *et al.* 1997; Meng *et al.* 2004; Xu and Norell 2004). We therefore considered each of the three possible theropod parental care states on each of the eight tree topologies described previously (i.e. 24 reconstructions examined in total). Data on parental care for each avian taxon were taken from the *Handbook of the Birds of the World* series when possible (del Hoyo *et al.* 1992–2004) or from more specific literature in the case of many passerine families (sources available on request). Many taxa have two or more character states seen commonly ($\geq 5\%$ on of species) among the species within that group and these taxa were assigned all such states (i.e. they are polymorphic).

We follow Tullberg *et al.* (2002) in assuming that uniparental care evolved from no care and only then to biparental care (i.e. it is unlikely that biparental care evolved directly from no care) and that uniparental care of one type cannot directly evolve into uniparental care of the other type (i.e. no cases of male-only care evolving to female-only care and vice versa) but must instead evolve through biparental care.

MacClade (version 4.08, Maddison and Maddison 2005) was used to reconstruct ancestral character state patterns. We assumed no specific character optimization (i.e. ACCTRAN, DELTRAN) since our goal is to examine the broadest range of most parsimonious ancestral state reconstructions.

Our reconstructions indicate that the relative placement of outgroups and the assumptions made concerning theropod parental care have a major impact on the most parsimonious reconstruction for the ancestral care state in birds. Whether we used the Sibley and Ahlquist tree or our composite tree had no impact on the ancestral state reconstruction; therefore, we only consider the twelve basic reconstruction patterns seen on one of these avian trees. When theropods are assumed to have shown either female-only or biparental care, then biparental care is reconstructed as the ancestral state in all eight reconstructions. However, when theropods are assumed to have shown male-only care, then one of four reconstructions show male-only care as the ancestral state with an equally parsimonious determination of either male-only or biparental care as the ancestral state for the remaining three reconstructions. Male care is unambiguously determined as the ancestral state when theropods are assumed to be the sister group to birds and turtles are a basal reptilian lineage (Figs. 9.1, 9.2). The remaining three reconstructions also support the possibility of ancestral male-only care in birds, regardless of assumptions concerning the theropod ancestry of birds or the different positions of the squamate and turtle lineages.

Burley and Johnson (2002), citing Tullberg *et al.* (2002), state that there is little phylogenetic support for the male-only care first hypothesis. Although most of our reconstructions support the evolution of biparental care as the



Fig. 9.1 Sibley and Ahlquist (1990) tree showing, superimposed, the reconstructed pattern of parental care evolution. This reconstruction assumes that theropods are the sister group of birds and that they showed male-only parental care. The ancestral state for birds in this reconstruction is male-only care. Original.

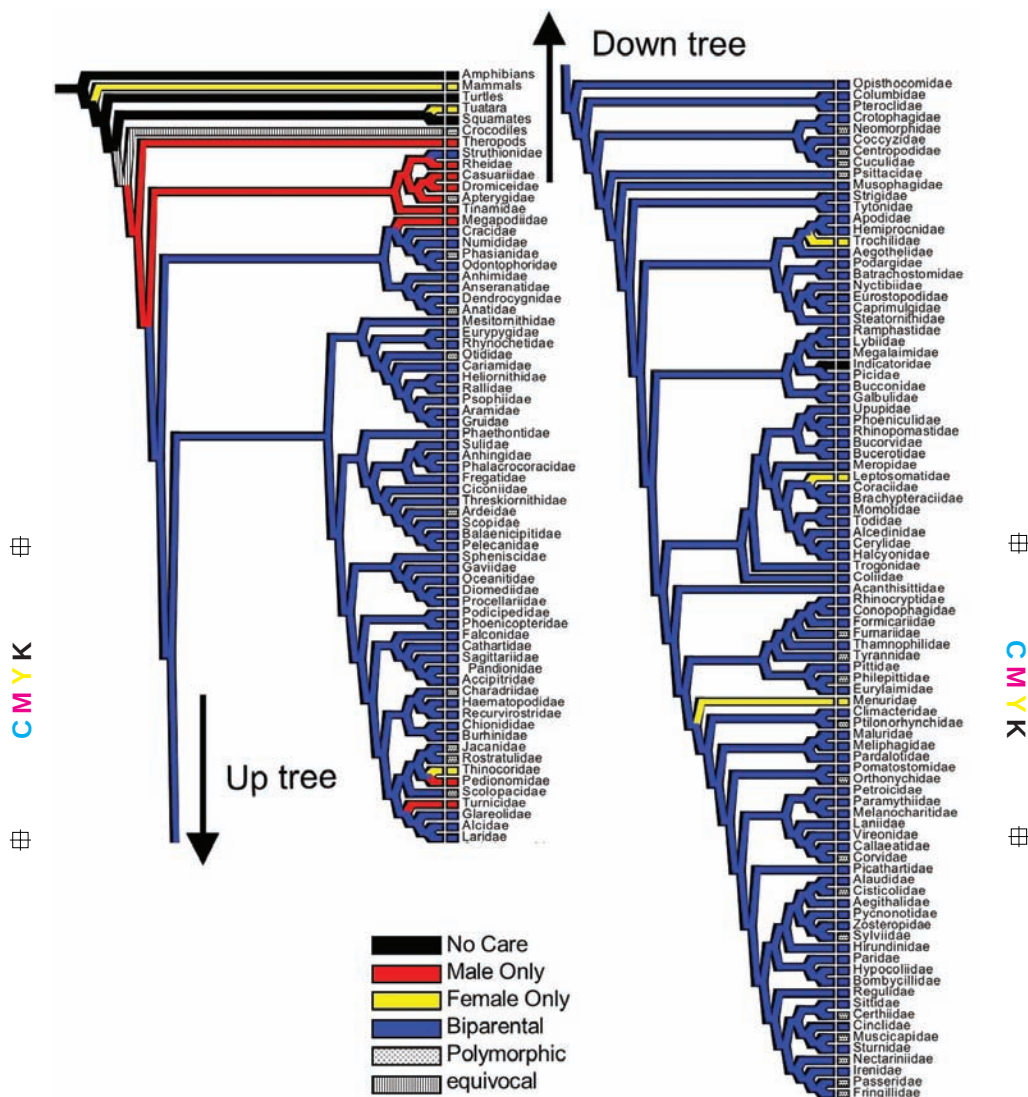


Fig. 9.2 Composite tree derived from the general consensus phylogeny of Cracraft *et al.* (2004, Figure 27.10) with additional resolution in the passerines from Barker *et al.* (2002) and Ericson *et al.* (2002). All remaining polytomies were resolved arbitrarily to allow full reconstruction of the parental care evolutionary patterns. As in Fig. 9.1, reconstruction assumes that theropods are the sister group of birds and that they showed male-only parental care. The ancestral state for birds in this reconstruction is male-only care. Original.

ancestral state in birds this is unlikely to be true, for reasons discussed above. Additionally, four of twelve reconstructions did indicate male-only care as a possible ancestral state. More definitive information concerning tetrapod

phylogeny, including the exact ancestry of birds, and, most importantly, the sex of the parent providing care in theropod lineages is needed to resolve this issue.

Wesolowski (1994, 2004) has questioned the legitimacy of assuming homology in parental care states between different bird groups and their outgroup lineages. However, it is common practice in phylogenetic studies to assume a trait's homology in the absence of evidence of homoplasy, and then investigate its degree of phylogenetic structure in the context of other traits (Hennig's Auxiliary Principle, Wiley *et al.* 1991). Additionally, there is no indication that behaviors *per se* are less reliable in evolutionary studies than morphology or molecules (de Queiroz and Wimberger 1993; McKittrick 1992). Also, several lineages in this analysis show extreme evolutionary stasis in parental care states (e.g. crocodylians (Shine 1988), theropods (see previous section on fossil data), ratites with male-only care (Ligon 1993, 1999), biparental care in most avian lineages (Tullberg *et al.* 2002)), which indicates the potential for parental care homology among these lineages. The shorebirds appear to be the only major exception to this pattern and show considerably more evolutionary change among parental care modes (Székely and Reynolds 1995; Reynolds *et al.* 2002)

9.3.3 Ecological Correlates of the Evolution of Male-only Care

Male-only care is rare in contemporary bird groups. However, in the 11 families where it is found (primarily the paleognaths and some shorebirds; Ligon 1999; Owens 2002) male-only care shows considerable evolutionary stasis (*sensu* Burt 2001) (Table 9.1). Comparisons of closely related shorebird species with male-only care show considerable ecological diversity and no ecological correlates for the evolution or maintenance of male-only care (Elzanowski 1985; Ligon 1993, 1999; Reynolds and Székely 1997; Owens 2002). Owens (2002) did find one pattern: species in families with male-only care were characterized by lower nesting densities than those in families with female-only care. Owens argues that in dense populations males have more chances for additional matings by abandonment and that females then face the 'cruel bind' (Trivers 1972) of uniparental care. Females, however, gain in situations of low nest density by abandonment and remating to produce additional clutches, while males assume uniparental care since they have no significant chance of obtaining additional matings.

9.3.4 Evolutionary Stasis and Transition Biases in Parental Care Evolution

Given the degree of evolutionary stasis demonstrated in parental care systems, a logical question is whether transitions between different forms of parental care, when they do occur, are seen with equal frequency or if there is evidence of certain transition biases. For example, once parental care evolved in birds, the evolution of egg and nestling characteristics further necessitated

Table 9.1 Average number and range (minimum and maximum) of branches showing either stasis (dark cells) or unambiguous evolutionary transitions for each parental care state across all reconstructions examined for the Sibley and Ahlquist and composite trees respectively. Counts do not include changes within polymorphic taxa. Each row in each cell represent different assumptions concerning the theropod parental care state: plain text = male care, bold = female care, italics = biparental care.

	To: Male	Female	Biparental
From: Male	8 (7-10), 10 (9-12) 7, 9 <i>7, 9</i>	0 0, 0 <i>0, 0</i>	1.25 (1-2), 1.25 (1-2) 1, 1 <i>1, 1</i>
Female	0, 0 0, 0 <i>0, 0</i>	0, 0 3 (1-5), 3 (1-5) <i>0.5 (0-1), 0.5 (0-1)</i>	0, 0 0.5 (0-1), 0.5 (0-1) <i>0.25 (0-1), 0.25 (0-1)</i>
Biparental	3, 3 4, 4 <i>4, 4</i>	3, 4 3, 4 <i>3, 4</i>	266, 284 267, 285 <i>270 (269-271), 288 (287-289)</i>

some sort of parental care in all subsequent avian lineages (van Rhijn 1984; Wesolowski 1994). This assertion is supported by the fact that, with the exception of some (but not all, as discussed above) megapodes, no other avian lineage has evolved to the state of no care. This pattern represents the most obvious transition bias seen in avian parental care evolution. Even lineages for which the biological parents provide no parental care, the brood parasites, have evolved elaborate ways to insure their young are cared for by other individuals.

Burley and Johnson (2002) regard such inferences of transition biases in evolutionary patterns as unreliable; however, they are willing to accept the ancestral character reconstructions of Tullberg *et al.* (2002) in support of their claim that biparental care is ancestral in birds. We fail to see the logic of accepting reconstructions of ancestral character states on the one hand, while ignoring patterns of evolution to understand how certain evolutionary transitions are more probable than others.

Understanding evolutionary transition patterns are relevant to the discussion of the probable ancestral state for birds. Some have argued that male-only care may be a likely candidate for the ancestral state for birds simply on the grounds that all other forms of parental care can easily evolve from this point (van Rhijn 1984; Handford and Mares 1985). In contrast, the evolution of biparental care may be more difficult from a female-only care system assuming it may be difficult to make it worth the while of males to join in parental care duties. Indeed, female-only care systems may represent a dead end to the evolution of other care systems in birds (van Rhijn 1984, 1990; Wesolowski 1994; Ligon 1999). Transitions from no care to female care are

common in a variety of vertebrate taxa (anurans, live-bearing teleosts, elasmobranchs, and squamates); however, female-only to biparental care transitions are seen frequently only in primates (Reynolds *et al.* 2002). Vehrencamp (2000) determined that male-only incubation twice gave rise to some form of shared incubation, but that female-only incubation has never evolved into shared incubation.

Our data provide only weak support for these interpretations. First, they suggest that the evolution of biparental care from uniparental care has been rare when one considers the number of unambiguous evolutionary transitions across all reconstructions (Table 9.1). Additionally, when biparental care has evolved, there are apparently only a few more cases derived from male-only care than from female-only care.

The appearance of monogamy and extensive biparental care probably made possible the evolution of altricial young in birds (Silver *et al.* 1985; Burley and Johnson 2002). However, altricial development has probably served as a subsequent evolutionary constraint (*sensu* Burt 2001) to the evolution of other mating and parental care systems due to the need for intensive feeding of young in most avian lineages (Silver *et al.* 1985; Ligon 1999). Even when ecological conditions make uniparental care sufficient for the successful production of young, the potential for the subsequent evolution of each form of uniparental care from biparental care systems depends on whether both sexes retain all parental care behaviors or have evolved specialized care duties. Evolution from biparental to male-only or female-only care systems is probable only when both sexes retain all parental care abilities (i.e. incubation, brooding, feeding young) (Trivers 1972; van Rhijn 1990; Ligon 1993). Vehrencamp (2000) reconstructed eight transitions from shared incubation in birds to some form of uniparental incubation. These transitions were biased toward female-only incubation (six of eight) and would probably have been even more strongly biased had they included transitions within the passerines. Our reconstructions, however, show no bias toward the evolution of female-only care or male-only care from an initial state of biparental care (Table 9.1).

Our data show no patterns of transition bias at this phylogenetic scale; however, additional consideration of potential transition patterns is warranted. First, Figures 9.1 and 9.2 show that most transitions in the trees examined here are to some form of uniparental care and that these transitions are typically restricted to terminal branches of species-poor groups. Hummingbirds are the only major exception. This pattern suggests that the evolution of either male-only or female-only parental care systems represents an evolutionary dead end. Finally, numerous taxa in our analyses are polymorphic and additional analyses within these groups may help resolve the issues of potential transition biases and the evolutionary potential for subsequent lineage-specific diversification associated with different parental care systems.

The shorebirds provide an example of such additional analyses. Transition biases in parental-care states of shorebirds have been investigated in detail (Székely and Reynolds 1995; Reynolds *et al.* 2002). Conclusions vary depending on whether biparental care is defined more restrictively as extensive parental contributions by both sexes or as situations in which one sex provides some care before abandonment. With a restrictive definition, Székely and Reynolds (1995) concluded that biparental care was ancestral for shorebirds with subsequent transitions to uniparental care biased toward male-only care. Transitions from male-only care to either biparental or female-only care were common yet there were few to no transitions from female-only care to either male-only or biparental care. When biparental care is defined more broadly, Reynolds *et al.* (2002) maintained the position that biparental care is ancestral for shorebirds. However, they found comparable numbers of subsequent transitions to male-only and to female-only parental care systems with no reversals to the ancestral state of biparental care.

We now turn our attention to another system of caring for young in which individuals in addition to the biological parents provide regular care. This system is termed cooperative breeding and is seen in numerous avian lineages. We review the conditions for the evolution of this system and the patterns of its subsequent evolution.

9.4 COOPERATIVE BREEDING

Among birds, one of the most interesting and most debated aspects of parental care is the phenomenon of cooperative breeding (Brown 1987; Stacey and Koenig 1990; Koenig and Dickinson 2004). Cooperative breeding is something of a catch-all label which includes a number different mating and social systems. As we view it, cooperative breeding is best defined as a social system containing not only breeding individuals (often only one female and one male) but also non-breeding nest helpers within a cohesive group. Although helpers are typically the offspring of one or both members of the breeding pair, group members unrelated to the young birds they provision are not rare. In both cases helpers provide food and other forms of care to nestlings that are not their offspring. This behavior is often referred to as alloparental care. Alloparental care in cooperative breeders is the behavioral manifestation of a stimulus-response interaction (begging nestling-food provisioning) between chicks and adult non-parent group members. The evolution of intense parental care was a requisite first for the evolution of altriciality, and second for the evolution of cooperative breeding (Ligon and Burt 2004).

Traditionally (over the past 30 years or so), two issues have captured the attention of students of cooperative breeding: (1) why do helpers feed chicks that are not their own offspring and (2) why do young birds, or some of them, not disperse when reaching physiological maturity? More recently, a third issue — the evolutionary or phylogenetic history of cooperative breeding — has

come to be recognized as a critical issue (Russell 1989; Peterson and Burt 1992; Edwards and Naeem 1993; Ligon 1993, 1999; Burt 1996; Cockburn 1996, 2003; Ligon and Burt 2004). Here we briefly treat two of these three topics: the origins of cooperative breeding as manifested by the feeding of chicks, and its evolutionary history. For assessments, evaluations and discussions of the main hypotheses pertaining to dispersal and natal philopatry in cooperatively breeding species, see Stacey and Ligon (1987, 1991), Koenig *et al.* (1992), Ekman *et al.* (2004), Dickinson and Hatchwell (2004) and Doerr (2004).

9.4.1 Origins of Cooperative Breeding

Cooperative breeding may initially have arisen more or less incidentally in response to the evolution of altricial young, together with the existence of factors that favored group living. Because altricial young demand intense parental care, natural selection promoted the development of a 'hard-wired' feeding response to the stimulus of begging chicks. When group living was favored, for whatever reason or reasons, this provided the opportunity for all individuals, both breeders and non-breeders, to respond to the stimulus of begging young. Not surprisingly, cooperative breeding occurs far more frequently in lineages having altricial development than would be expected if these traits evolved independently (Ligon and Burt 2004).

With the passage of evolutionary time, cooperative breeding in some lineages became a refined adaptive response to certain environmental and social conditions. Thus the importance of cooperative breeding varies from species to species, ranging from an 'obligate' condition in which helpers are always present and are required for successful production of young birds, to incidental, in which helpers are infrequent or rare, and no selective benefit of helping has been identified (Ligon and Stacey 1989, 1991; Ligon and Burt 2004).

9.4.2 Kinds of Care Donated by Helpers

Helping behavior by non-breeders is basically similar to parental behavior and must have the same evolutionary origins and genetic bases. After all, unlike the eusocial insects, every non-breeding helper has the potential to become a parent and many eventually do so. The evidence for a hard-wired stimulus-response component to the care-giving behavior both of parent birds and the non-breeding helpers is evidenced by the surprisingly frequent occurrence of interspecific feeding and the exploitation of the feeding response by social or brood parasites (Ligon and Burt 2004).

In addition to feeding nestlings and fledglings, helpers of some species incubate eggs, brood chicks, remove fecal matter from the nest and attempt to protect the young birds from potential predators. Commonly, the role of helpers of one or both sexes is very similar to the role exhibited by the parent bird of the same sex. For example, in *Picoides borealis*, the Red-cockaded Woodpecker, the male breeder incubates the eggs and broods small nestlings,

and male helpers exhibit these same parenting behaviors (Ligon 1970; Conner *et al.* 2001).

9.4.3 Geographic and Phylogenetic Patterns of Cooperative Breeding in Passeriform Birds

The distribution of avian cooperative breeding is of special interest and significance on two counts. First, there is its geographic distribution, and second, there is its phylogenetic distribution. Although at first glance these may appear to be very different issues, they are intimately related. Whereas geographic distribution has been repeatedly analyzed and written about, the phylogenetic distribution has been considered for many fewer years.

9.4.3.1 Geographic patterns

Cooperative breeding occurs most commonly in tropical or subtropical regions. Australia, in particular, can be viewed as the 'cooperative breeding capital of the world'. Many studies have attempted to identify key ecological factors that promote the frequency of cooperative breeding on that continent and elsewhere, but with little success (Heinsohn *et al.* 1990; Cockburn 1996, 2003).

For example, Ford *et al.* (1988) suggest that in Australia cooperative breeding is favored by aseasonal environments, whereas Du Plessis *et al.* (1995) conclude that in South Africa cooperative breeding is associated with seasonal environments. With regard to these apparently contradictory conclusions, Ligon and Burt (2004) suggest that both of these southern hemisphere environments, which are benign or permissive as compared to highly seasonal ones, allow the retention of cooperative breeding that had evolved in the ancestral species.

With regard to suggestions that something special about the Australian environment has led to the relatively frequent occurrence of cooperative breeding on that continent, Cockburn (1996) found that within the Corvida (Fig. 9.3) the proportion of clades originating outside Australia that contain at least one cooperatively breeding species is similar to the pattern in Australia-New Guinea. Thus there is probably no special environmental factor within Australia that has promoted cooperative breeding.

Rather, cooperative breeding is unusually common in the Corvida, wherever they occur. Moreover, no environmentally based model can apply to many cooperative breeders in Australia because they occur in a wide variety of densities and habitats, yet are cooperative throughout their ranges (also see Cockburn 2003).

To summarize, the relative frequency of cooperative breeders in Australia and other tropical and subtropical regions today is not due to special environmental factors that promote the repeated evolution of this social system. Rather, cooperative breeding evolved long ago in a less climatically severe world and has been retained to the present time in those regions



Fig. 9.3 Sibley and Ahlquist (1990) tree showing reconstructed pattern of cooperative breeding evolution. Original.

characterized by a benign, aseasonal climate as compared, for example, to the strong seasonality of the Holarctic region.

9.4.3.2 Phylogenetic patterns

Recent phylogenetic reconstructions based on nuclear DNA sequence data have indicated that passerine birds originated in Gondwanaland (Barker *et al.* 2002, Ericson *et al.* 2002). Thus some of the oldest living passerine lineages

include the New Zealand 'wrens', Family Acanthisittidae, and the 'old endemic' families, basically including the Corvida of Sibley and Ahlquist (1990). A high percentage of the living species of these two groups exhibit cooperative breeding. Because cooperative breeding occurs in the Acanthisittidae, the sister group to all other passeriform birds, as well as in the oscine and suboscine passerines, it appears to be a basal trait for the order (Fig. 9.4). Moreover, contradicting the conclusions of Sibley and Ahlquist (1990), the Passerida appear to be derived from the ancient Australian passeriform birds within the now paraphyletic Corvida (Barker *et al.* 2002, Ericson *et al.* 2002).

In addition to the studies of Barker *et al.* (2002) and Ericson *et al.* (2002), which only imply that cooperative breeding is an ancient trait in passerine birds, Cockburn (2003) states more directly that cooperative breeding "... is the predominant social system of some ancient oscine clades". Finally, Ligon and Burt (2004) mapped cooperative breeding on the phylogeny of Sibley and Ahlquist (1990) and independently came to a similar conclusion, namely that cooperative breeding is probably the basal condition in the order Passeriformes (Fig. 9.3).

Two additional points derived from this last analysis also stand out. First, altriciality is ancestral in the Neoaves beyond the Parvclass Galloanserae. Second, based on the Sibley and Ahlquist (1990) tree, cooperative breeding may be ancient, occurring in many of the oldest of living altricial neoavian families (Fig. 9.3).

Although a large percentage of the Old Endemics of Australia exhibit cooperative breeding, this is not the case for the Passerida, which has primarily radiated and diversified following dispersal from the Australian region into the Holarctic. Added to the interest of this geographic-evolutionary scenario is the fact that no species of Passerida currently occupying Australia is a cooperative breeder, despite the facts that the early ancestors of this group probably exhibited that trait, and that it is prevalent in some contemporary groups of this huge category of birds outside of Australia. In such groups, as well as in certain non-passeriform lineages, the presence of cooperative breeding probably is a re-expression of a trait that evolved deep within the avian tree. For example, cooperative breeding occurs as a phylogenetically isolated event in some genera.

Woodpeckers may be one of the most ancient of living neoavian birds (Sibley and Ahlquist 1990; Jamieson, Volume 6A, Chapter 8), and it appears that cooperative breeding is an ancient trait in woodpeckers as well as in most of their closest relatives (Ligon and Burt 2004) (Figs. 9.3, 9.4). Cooperative breeding apparently occurs in at least four genera of woodpeckers, but, based on current knowledge, it is not very common in this large group. It may be a 'primitive' trait in some genera (e.g., *Melanerpes*) and a derived trait in others (e.g., *Picoides*). For example, the Red-cockaded woodpecker is the only member of the latter genus known to engage in cooperative breeding and the specific ecological factors promoting the development (re-emergence) of this social system are unusually well understood (Ligon, 1993, 1999).



Fig. 9.4 Composite tree derived from the general consensus phylogeny of Cracraft *et al.* (2004, Figure 27.10) with additional resolution in the passerines from Barker *et al.* (2002) and Ericson *et al.* (2002). All remaining polytomies were resolved arbitrarily to allow full reconstruction of the pattern of cooperative breeding evolution. Original.

9.4.3.3 The Phylogenetic distribution of cooperative breeding in bee-eaters, family meropidae

Phylogenetic analyses can help us to understand the history of cooperative breeding in many avian groups. An example of this approach is provided by the Family Meropidae, the bee-eaters (Burt 1996).

Bee-eaters comprise a largely morphologically uniform avian family widely distributed in the Old World tropics and subtropics. They are also uniform in certain basic aspects of their reproductive biology. For example, all 26 species excavate nest cavities in soil, all lay unmarked white eggs, and all exhibit biparental care of eggs and chicks. However, social systems vary, in that some species nest in colonies, while others breed as solitary pairs, and some species are cooperative breeders while others are not. These two traits, coloniality/non-coloniality and cooperative breeding/non-cooperative breeding, appear to be causally related.

Of the 26 species in the Family Meropidae, 17 species are known or likely to be cooperative breeders. Five species apparently are not. At least one species shows variation among populations in its breeding system. The breeding systems of the remaining three species are unknown. Reconstructions on six alternative trees (Burt 1996) indicate one of two basic patterns of breeding system evolution (Fig. 9.5). Cooperative breeding is an ancient trait that evolved either before the diversification of the entire family or before the diversification of the genus *Merops*.

Merops bee-eaters are widely distributed over the paleotropics and southern Eurasia. Throughout this range they occupy a variety of habitats including tropical forests, grasslands, marshes, savanna woodlands, semi-desert and cultivated areas. They also vary greatly in their nesting substrates, from flat ground to cliff banks, and differ in their migratory behavior. These traits generally show no correlation with breeding systems within the family (Burt 1996), with one exception: colonial versus solitary nesting. Species that nest in solitary-only situations have evolved non-cooperative breeding from a cooperative breeding ancestor more often than one would expect if degree of sociality and breeding system evolved and were maintained independently of each other (Fig. 9.5).

The general pattern of evolutionary stasis, with cooperative breeding retained in the majority of lineages, can be explained in one of two ways. First, individuals in colonial species may be more likely to exhibit alloparental care simply because they are in close association with begging young. In addition, cooperative breeding may be adaptive in certain colonial species and natural selection may maintain and refine helping behavior (Emlen 1990; Jones *et al.* 1991). Determining the adaptive or non-adaptive nature of alloparental care in other colonial species of bee-eaters will require additional research.

9.5 CONCLUSIONS

Biparental care is often assumed to represent the ancestral state for birds because of its predominance in contemporary lineages and some phylogenetic studies support this conclusion. However, there is also phylogenetic support for the conclusion that the ancestor of birds showed male-only parental care. Additionally, there are ecological reasons to support the latter interpretation. Ancestral female birds probably laid large eggs for the production of precocial

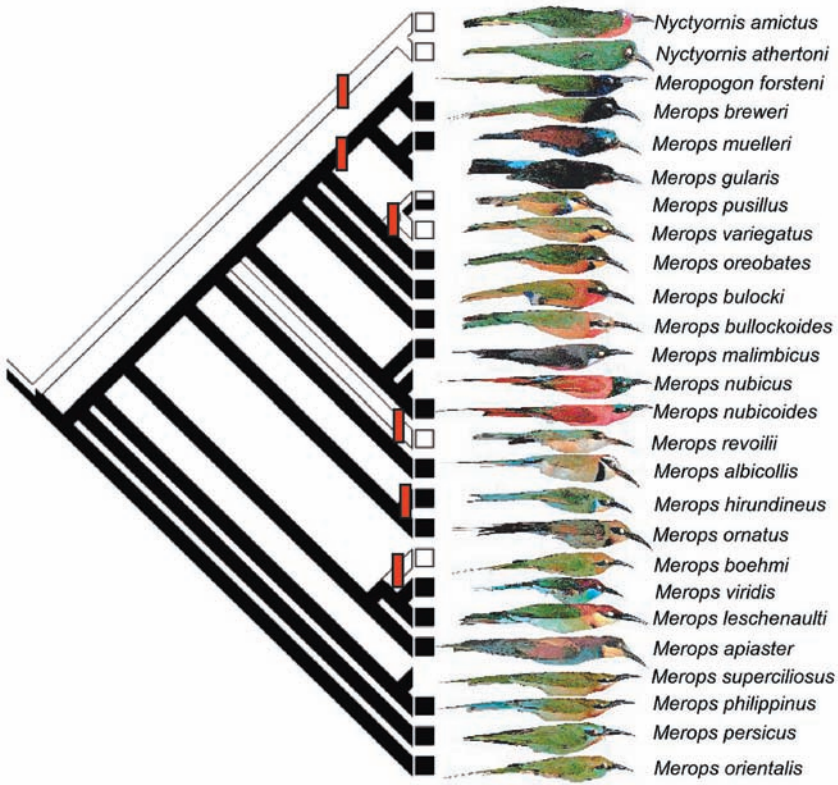


Fig. 9.5 Phylogeny of bee-eaters showing patterns of evolution in cooperative breeding and nesting density (tree drawn using Mesquite v 1.06, Maddison and Maddison 2005). Cooperative breeding (black branches) evolved early in the diversification of this family with three to five reversals to non-cooperative breeding. Evolution of non-cooperative breeding was concentrated in lineages that had evolved solitary nesting (red dashes) from a colonial nesting ancestral state. Modified from Burt (1996).

or superprecocial young. Formation of a clutch of these eggs demanded intense foraging effort that precluded females from providing nest guarding behavior. However, relative to males, this behavior signified minimal costs and potential fitness benefits via increased offspring survival and possibly increased mating options. The key to resolving this issue lies in firmly establishing which lineage is the sister group of birds, the ecological and physiological conditions (nest densities, diet of adults and young, developmental mode, sexual dimorphism, etc.) in which they existed and the sex of individuals providing parental care. To say the least, these data will not be easy to obtain.

Patterns of subsequent evolution in parental care systems and how these systems have co-evolved with developmental modes, mating systems and

social systems, and under what ecological conditions, should be explored in more detail as our phylogenetic hypotheses become more refined and better resolved. One possible evolutionary pattern shown here concerns the phylogenetic placement of lineages that have reverted to fixed uniparental care systems. Most of these lineages show low rates of diversification. More detailed analyses will be needed to test the idea that uniparental care tends to represent an evolutionary dead end for these lineages.

Cooperative breeding might be considered as the epitome of parental care in birds, in that extensive and often highly specialized care of chicks is conducted by non-breeding individuals. Cooperative breeding appears to have evolved early in the ancestors of many contemporary avian lineages and in many cases to have been maintained and refined throughout much of the Cenozoic. Currently, it is found primarily in relatively warm, subtropical or tropical regions. In terms of the percentage of species exhibiting cooperative breeding, Australia is the center of its distribution. Australia appears to be the ancestral home of the passeriform birds and is home to most members of the Parvorder Corvida, which contain a high percentage of cooperative breeders. The Corvida gave rise to the Parvorder Passerida, which has become numerically dominant in the Holarctic, although cooperative breeding has been lost in most of the temperate zone species comprising it.

Many other non-passeriform families are also characterized by cooperative breeding. A prime example is the bee-eaters, Family Meropidae, in which most species exhibit this social system. As in the passeriform birds, cooperative breeding appears to be an ancient trait in the bee-eaters, appearing very early in the evolutionary diversification of the family.

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Brood Parasitism in Birds

Oliver Krüger and M. de L. Brooke

10.1 INTRODUCTION

Recent years have witnessed an explosion of interest in the subject of brood parasitism, an explosion that has, we suggest, received crucial catalysis from two directions. Firstly, some 30 years ago Stephen Rothstein (Rothstein 1975a) realized that the behavior of birds that were potential hosts of cowbirds could be explored by placing model eggs into their nests. This proved a powerful technique for exploring many of the subtle coevolutionary interactions between parasites and hosts, and has since been widely adopted by other workers. As the complexity of these interactions has become appreciated, so evolutionary modelers have entered and contributed to the field. Secondly, refined DNA techniques have allowed the more reliable determination of the occurrence of intraspecific brood parasitism and hence the asking of more precise questions about its occurrence (McRae and Burke 1996). Considering first intraspecific and then interspecific brood parasitism, our chapter focuses on coevolutionary interactions associated with these phenomena.

10.2 TAXONOMIC OVERVIEW OF INTRASPECIFIC BROOD PARASITISM

If individual birds are seeking to enhance their reproductive success beyond what can be achieved by breeding in a pair, or more rarely, a group, then there are two obvious avenues. Males can engage in extra-pair mating and DNA-based studies suggest that, in the majority of species, a proportion (up to 80%) of broods will contain young fathered by other than the pair male (Bennett and Owens 2002). Females facing the cost of producing extra eggs, as opposed to the males' lesser cost of sperm production, may be more constrained, and so the tactic of laying one or more eggs in the nests of other females is not especially common among birds. In fact the tactic of intraspecific brood parasitism (IBP), where a female lays one or more eggs in another's nest and

then plays no part in subsequent incubation and rearing of young has been reported in 236 species, approximately 2.4% of all species (Table 10.1, Yom-Tov 2001).

Table 10.1 The number of species in the various orders of birds, following Clements (2000) who includes the turacos within the Cuculiformes, and the number of species in which IBP has been reported, following Yom-Tov (2001).

<i>Order</i>	<i>Number of species</i>	<i>Number of species where IBP reported</i>	<i>Percentage</i>
Struthioniformes	10	2	20.0
Tinamiformes	47	2	4.3
Sphenisciformes	17	0	0
Gaviiformes	5	0	0
Podicipediformes	19	6	31.6
Procellariiformes	110	2	1.8
Pelecaniformes	66	0	0
Ciconiiformes	122	5	4.1
Phoenicopteriformes	5	1	20.0
Anseriformes	160	74	46.3
Falconiformes	307	1	0.3
Galliformes	282	32	11.3
Opisthocomiformes	1	0	0
Gruiformes	204	8	3.9
Charadriiformes	348	20	5.7
Pterocliiformes	16	0	0
Columbiformes	308	9	2.9
Psittaciformes	352	0	0
Cuculiformes	161	5	3.1
Strigiformes	204	0	0
Caprimulgiformes	116	0	0
Apodiformes	437	2	0.5
Coliiformes	6	0	0
Trogoniformes	39	0	0
Coraciiformes	209	1	0.5
Upupiformes	10	0	0
Piciformes	409	0	0
Passeriformes	5781	66	1.1

The list of species assembled by Yom-Tov could be inflated by species where IBP is rare and essentially accidental. On the other hand ornithologists may have failed to record the tactic among species which are little-studied or where the tactic is infrequent. Thus intraspecific brood parasitism is much less common than extra-pair mating but rather more common than interspecific brood parasitism, the tactic of the 100 or so species discussed in the later part of this chapter.

IBP is distinct from another alternative mating strategy termed quasi-parasitism, where a female lays an egg in another female's nest and that egg has been fertilized by the male partner at the parasitized nest. Recently

reviewing quasi-parasitism in birds, Griffith *et al.* (2004) recorded it in a maximum of 12 species. It may be rare because only in fairly restricted circumstances do the benefits to the host male of paternity outweigh the costs of parasitism (Lyon *et al.* 2002).

The very detection of IBP is problematical. Before the advent of DNA-based techniques allowing the certain determination of the mother of every egg in a clutch, albeit at a non-trivial cost of time and money, detection was indirect. Firstly, if there were irregularities in the laying sequence, in particular if two eggs appeared on one day, then, since no species lays eggs faster than one a day, IBP was presumed. This line of evidence obviously does not work if the laying parasite removes a host egg at the same time as she lays her own in the host nest. Secondly, the appearance of an egg oddly colored in comparison to others in the female's clutch could be indicative of IBP. However, the reliability of this strand of evidence which, at best, is most useful for species with patterned eggs, has been questioned (McRae 1997). Its value is further undermined by the fact that females of some species may lay an oddly-colored egg last in the clutch, thereby signaling clutch completion either to themselves (Davies 2000) or to would-be parasites (Ruxton *et al.* 2001). Thirdly, comparison of maternal and chick proteins may reveal chicks that have hatched from parasitic eggs (Andersson and Åhlund 2000), but the estimated proportion of parasitic chicks is likely to be lower than the true value because some parasites and hosts will share proteins (Romagnano *et al.* 1989). Finally, the release of an egg from an ovary leaves a tell-tale scar. Counting such scars, unfortunately involving the sacrifice of a female, will reveal whether the number of scars is fewer than the eggs seen in the nest. If it is, IBP is strongly suspected (Kennedy *et al.* 1989).

A striking feature of Table 1 is the absence of IBP from some orders, for example the 352 species of Psittaciformes (parrots) and the 204 Strigiformes (owls), and its relatively high prevalence in some other orders, most conspicuously the Anseriformes (ducks and geese) but also, to a lesser degree, other orders with precocial chicks such as the Podicipediformes (grebes) and Galliformes (gamebirds). What features link the groups where IBP is either unusually prevalent or absent?

Lyon and Eadie (1991) as well as Yom-Tov (2001) noticed that IBP is associated with precocial young, and precocial young are associated with larger clutch sizes (Lack 1968, but see also Bennett and Owens 2002). This makes sense on several grounds. A female laying many eggs has more opportunities to foster at least part of her output onto conspecifics, while the marginal cost of accepting and incubating extra eggs may be lower for a host female with a multi-egg clutch than for a female with a small or single-egg clutch. Furthermore, where the species' clutch size is large, the time window in which a parasitic egg can be successfully added to the host clutch is longer (Geffen and Yom-Tov 2001).

A priori, one might predict IBP to be particularly prevalent among species where other females' nests are easily located and accessible. Such nest

characteristics, which would aid the parasite, are most obviously features of colonial nesters. Yom-Tov (2001) has noted how 46.5% of species where IBP has been reported are colonial breeders as compared to about 13% of all bird species. There clearly is a link between coloniality and IBP. Equally clearly, coloniality is not a sufficient condition for IBP since there are major groups of colonial birds (e.g. *Procellariidae*, *Alcidae*) where no cases of IBP have been reported. A difference between colonial nesters with IBP and those without is clutch size. Although the point needs critical analysis, clutch size is apparently larger in the former group. In other words, colonial species with precocial young and large clutches are particularly likely candidates for IBP.

Species that are neither colonial nor associated with precocial young but in which IBP has been reported are found in four orders, *Columbiformes*, *Cuculiformes*, *Apodiformes* and *Passeriformes*. All 16 species among the former three orders nest in the open while, among the 16 non-colonial passerine species with reported IBP, five nest in cavities and two in closed nests. Since cavities suitable for nesting may be a limiting resource, this habit may be a further factor predisposing species towards IBP.

10.3 EXPLANATIONS FOR INTRASPECIFIC BROOD PARASITISM AND TESTS OF THE EXPLANATIONS

Can these generalized correlates of IBP help explain why some species, but only a fairly limited set, adopt the habit? Davies (2000) has outlined the broad classes of explanation which derive from asking when a female might gain greater lifetime fitness benefit by laying some or all of her eggs in another female's nest, rather than in her own.

- (i) Incubating eggs and rearing young is evidently a costly activity and therefore it could benefit a female to foist the task onto another host female. The benefits are likely to depend on the number of available host females, and so will decline the higher the proportion of females that i.e. opt for parasitism. At some frequency of parasitism the benefits of parasitism match those of caring for eggs in the normal manner, and a frequency-dependent equilibrium is potentially attained in a mixed evolutionarily stable strategy (ESS), see Fig. 10.1.
- (ii) A second class of explanations proposes that some females are unable to secure their own nest site, perhaps because of competition from conspecifics. Rather than abandon nesting altogether, it might pay such females to lay whatever eggs they can in the nests of other females. This is a 'best of a bad job' hypothesis or a conditional ESS (Fig. 10.1).
- (iii) The third class of explanations notices that, particularly in species with a staggered onset to incubation, the marginal value of each extra egg in a nest declines as the clutch size swells, for example because of competition among the hatchlings. In that circumstance it might benefit a female to lay any extra eggs she is capable of forming into other females' nests where they would, on average, contribute more to her

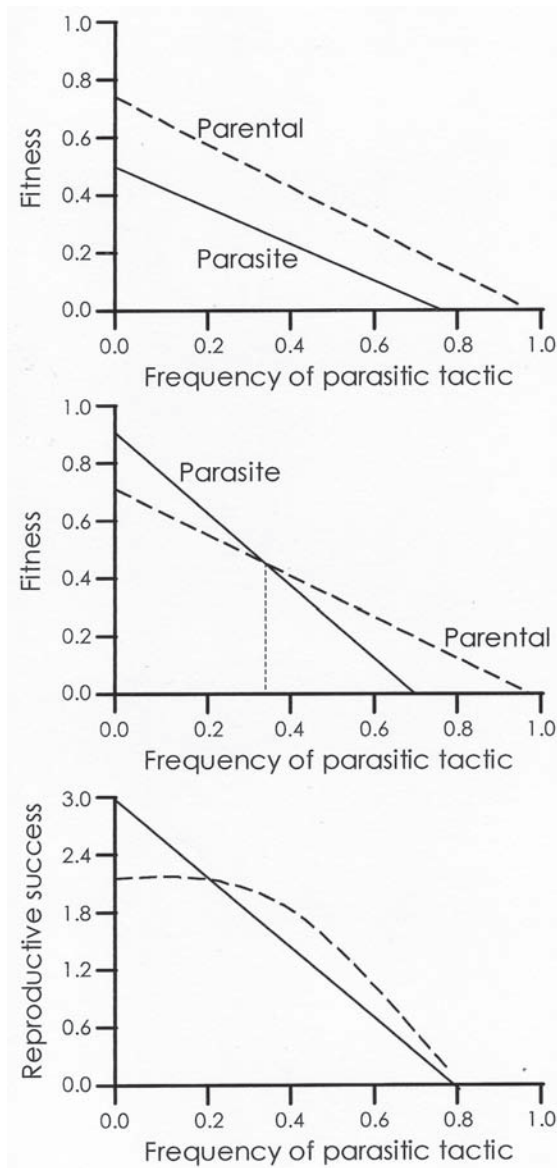


Fig. 10.1 Scheme representing intraspecific brood parasitism as a conditional ESS (top panel) where parasites are always less successful than parentals. The middle panel shows a mixed ESS where, at low frequencies, parasites are more successful while, at high parasite frequencies, parentals are more successful. The vertical dashed line shows the parasite frequency where parasite and parental strategies are equally successful. The bottom panel, based on Eadie and Fryxell's (1992) *B. islandica* data, shows an example of a mixed ESS, reproductive success of the two tactics varying according to the frequency of parasitism in this duck. Redrawn from Eadie, J. M. and Fryxell, J. M. 1992. *American Naturalist* 140: 621-641, Figs. 1 and 4.

fitness than would further eggs laid in her own nest. Thus undertaking some IBP is a means to enhance reproductive success. However it should be noted that this explanation is not completely independent of (i). The potential for enhancing reproductive success by IBP will partly depend on the behavior of other females in the population.

- (iv) A final idea is that, by laying in several nests, a female avoids having all her eggs in one nest (or basket!). While superficially attractive, a theoretical analysis (Bulmer 1984) has suggested that any benefit arises, not because selection is minimizing variance per se, but because selection maximizes the number of surviving offspring in the face of density-dependent survival. At this point, the idea has almost conflated with (iii). That said, it might be worthwhile to explore theoretically whether short-lived species would benefit more from spreading their eggs into several nests and avoiding complete reproductive failure in their short lives than would long-lived species which potentially have many reproductive attempts. A critical analysis would have to take account of the tendency for shorter-lived species to lay larger clutches, itself a factor associated with IBP.

Before discussing which of these explanations may apply, we will first consider the process of laying an egg in a conspecific's nest, as exemplified by several detailed studies, and the related issue of which members of population are the brood parasites.

It is a common observation by students of interspecific brood parasitism that, if it is to hatch, the egg must be laid at the correct time. If it is laid prematurely, more than a few days ahead of the start of the host laying sequence, then the host is able to employ the simple rule of thumb "That egg is premature; it cannot be mine; it should be rejected." If it is laid late, more than a few days after the start of host incubation, it will not have hatched by the time all the host eggs have hatched, and effective incubation has ceased. The same timing constraints generally apply to intraspecific parasites (Lank *et al.* 1989a; Pinxten *et al.* 1991; Whittingham and Dunn 2001). Exceptions to this rule are provided by the remarkable cases of the Cliff swallow (*Petrochelidon pyrrhonota*) (Brown and Brown 1988) and Cave swallow (*P. fulva*) (Weaver and Brown 2004) which occasionally carry in their bills partly-incubated eggs from their own nest to that of a conspecific whose clutch is at a similar stage of incubation. In such cases the parasitic egg is added to the host clutch well after the start of incubation and the proportion of nests containing such moved eggs is low, between about 1 and 6% (Brown and Brown 1988; Weaver and Brown 2004).

When laying in a host nest, the parasite often simply adds her own egg (e.g. wood duck (*Aix sponsa*), Semel and Sherman 1986, American coot (*Fulica americana*), Lyon 1993 and Moorhen (*Gallinula chloropus*), McRae 1996, Fig. 10.8A). Aside from the fact that these species have bills that may be ill-suited to grasping and removing a host egg, the young are precocial or semi-precocial and so the number of host young may have little impact on the fitness of the

parasite young. This means there may be little or no benefit to the parasite in removing an egg. Alternatively, some, but not all parasitic European starlings (*Sturnus vulgaris*) remove a host egg when laying their own. There is little evidence that hosts can count the number of eggs in their nest (but see Lyon 2003b) and so the advantage to the parasite of removing one host egg would be to minimize any reduction of incubation efficiency due to an enlarged host clutch and to reduce competition for food between the altricial young of parasite and host.

While there are, as described, features of the parasites' laying behavior that can be viewed as strategies for enhancing the success of their eggs, there are also strategic issues concerning which members of the population pursue parasitism in any year. In snow geese (*Anser caerulescens*), females which nest never lay parasitic eggs. The parasites are exclusively females which have failed to secure a suitable nest site, for example because of delayed snow melt, or have arrived on the breeding grounds with insufficient body reserves to nest normally (Lank *et al.* 1989b, 1990). In this case, the parasites appear to be making the best of a bad job (ii — above), and never fare as well as normally-nesting females. In other species, the picture is more complicated. McRae (1998) found that the parasitic eggs of *Gallinula chloropus* were laid by three distinct classes of female. Fifty-six percent of the parasitic eggs were laid by females, about a quarter of the population, which first laid one or more eggs in neighbors' nests before laying their own normal-sized clutch. This strategy enhanced their reproductive success (iii — above) by about 10% compared to females which laid only their own clutches. Nineteen percent of eggs were laid by females which, having lost their own nests to predation, were seeking to salvage some success by subsequent parasitic laying. And 25% of eggs came from females without territories at all; their strategy matched that of *A. caerulescens* discussed above. These last two strategies of *G. chloropus* are variations on the theme of hypothesis (ii).

While most bird species that combine parasitic and own-nest laying in the one season lay the parasitic eggs before proceeding to their own clutch, this pattern shows variability. Forman (2005) reported that, in a young and expanding *Gallinula chloropus* population with low predation, parasitic layings were as likely to be undertaken by females before as after they had laid their own clutches (however parasitic laying during clutch production remained rare). Thus the exact pattern of parasitic laying shows flexibility in response to ecological circumstances (see also Sorenson 1991, 1993).

If some females of a species have the capacity to enhance their breeding success by laying 'extra' parasitic eggs while others do not, this raises the question of whether the parasites are of higher quality. It is a plausible possibility which appears not to have been investigated thoroughly. The fact that *G. chloropus* females which lay parasitic eggs before depositing a clutch in their own nest and indeed rear more young because of this tactic suggests that indeed they are higher quality individuals. But the conclusion would be more secure if corroborated by other lines of evidence (e.g. higher annual survival of

parasites). Thinking along these lines raises further questions which have yet to be investigated extensively. For example, is a propensity for IBP inherited from the parents?

In longer-lived species which tend to be most fecund after several years of breeding, is the tendency to IBP a characteristic that, in any individual, is more or less fixed for life, or does it increase to a peak after several years of breeding, only to wane with the onset of senility? In support of these ideas, Lyon (2003a) found that parasitic *Fulica americana* females were older and laid more total eggs than non-parasitic females and, among parasites, older females laid more parasitic eggs. Another strategic possibility is that parasites lay higher quality eggs, to enhance the competitive abilities of their chicks, but one study that tested this idea in *S. vulgaris* found no support (Pilz *et al.* 2005).

While the scenarios described above have, in varying degrees, supported hypotheses (ii) and (iii), a remarkable study of the cavity-nesting duck, Barrow's goldeneye (*Bucephala islandica*), supports hypothesis (i). Probably because suitable cavities are in short supply, females in British Columbia opt either to behave as normal nesting parents, or to lay their eggs in the nest of another female. In each season the parasites generally lay their eggs in the site of just one nesting female, as opposed to several. However, while individuals generally stick to one tactic or the other in any one season, they can switch tactics between years, indicating that the two types of females do not belong to two distinct genetic groups. Eadie and Fryxell (1992) found that the benefits of parasitism declined as the percentage of parasites in the population increased (Fig. 10.1). This was because fewer fledglings per egg were produced from the very large clutches resulting when more than one parasite laid in a nest. Conversely, the success of parasites was higher than that of nesting females when parasitism was rare. The predicted frequency of parasitism was 0.17-0.23 (depending on the parasite's precise clutch size), which corresponded well to the observed parasitism frequency of 0.17 in the study population. However Eadie and Fryxell noticed that, when competition for nest sites was relaxed, in other words when there were more than sufficient cavities for all breeding females, then parasitic females were likely to fare less well than nesting females whatever the frequency of parasitism. Thus the benefit of the parasitic habit depended not only on the behavior of other individuals but also on the overall population density.

Eadie and Fryxell's study of frequency-dependent parasitism assumed that host nests varied in clutch size but in no other feature that might influence the benefits of parasitism. However, two factors which could affect the suitability of a nest for parasitism are whether it is secure from predators and whether host and parasite are related. We now discuss these factors.

All else being equal and ignoring the possibly greater search effort involved in finding a secure nest, a parasite is likely to gain greater benefit from depositing eggs in a nest that is secure from predation than in one that is exposed. Pöysä (1999) reported that Common goldeneye (*Bucephala clangula*) (Fig. 10.8B) nests were more likely to be parasitized if the site had not been

depredated during the previous attempt. A subsequent experimental study (Pöysä 2003) suggested that parasitic females do not base laying decisions on the basis of encountering broken eggs or nest disarray, both indicators of predation, at a nest site. Rather they prefer nest boxes on lakes where the real risk of predation is low, perhaps determined on the basis of their own prior experience. However, if all females have a similar preference, then the risk that parasites will interfere with one another, by laying in the same secure localities, increases.

10.4 ARE KIN PARASITIZED?

Whether intraspecific brood parasites should deposit their eggs in the nests of kin or non-kin is a complicated issue. While hosts may be more ready to accept eggs from relatives, because they will possibly gain indirect fitness benefits, parasites should avoid parasitizing kin if the parasitism imposes costs on the hosts (Lopez-Sepulchre and Kokko 2002). Andersson (1984, 2001) showed that kinship can promote brood parasitism, especially if perfect kin recognition is assumed. This assumption is probably unrealistic, and so Lopez-Sepulchre and Kokko considered the situation where kin recognition is not perfect and hosts do not always detect parasitism. When IBP imposes a cost on the host, a parasitic female that can choose should avoid parasitizing relatives, unless the costs are not too high and host can recognize relatives' eggs to the extent of rejecting them less often than the eggs of non-kin. Alternatively, if IBP benefits the host (see below), for example by diluting the risk that the young will suffer predation, then parasites should do their relatives a good turn, and parasitize them.

Studying *Bucephala clangula* in Sweden, Andersson and Åhlund (2000) confirmed that females are more likely to parasitize their birth nestmates (social mothers or sisters) than expected by chance. Because of parasitism in this population, such birth nest mates will not always be genetic relatives, but they are more likely to be so than random members of the population. Various lines of evidence suggested that this result was not simply a consequence of young females returning to breed where they were born, and encountering close relatives there. Particularly compelling was the observation that parasite-host relatedness was higher in nests where the parasite laid several eggs than in nests where she laid only one egg.

10.5 RESISTANCE TO INTRASPECIFIC BROOD PARASITISM

If IBP represents a cost to the host, then natural selection will favor hosts which resist parasites. This resistance can take various forms, which generally parallel the defenses shown by hosts against interspecific parasites. The ability of hosts to reject eggs mis-timed by several days has been mentioned above. Hosts also employ physical resistance to repel parasites. For example, McRae (1996) described how parasitic females in *Gallinula*

chloropus contended with pecks from the beak of either the host male or female (depending on which was on the nest at the time) as they laid. Perhaps surprisingly, the onslaught was never so intense as to drive the parasite from the nest before she laid. Davies (2000) wondered whether the hosts restrained themselves to reduce the risk of damaging their own eggs in the commotion.

Once the parasite egg is laid, the host could, at least in theory, reject it either by ejection from the nest, or by building over it, or by nest desertion, behaviors that would be exactly analogous to rejection of the eggs of interspecific parasites. In fact, rejection of conspecific eggs has been recorded in remarkably few species (Davies 2000), among seven passerine species (four weavers, *Fringilla coelebs*, *Fringilla montifringilla* and *Emberiza schoeniclus*) and two rails (*Fulica americana* and *Ortygometra carolinus*). All nine species have patterned eggs such that each individual female lays a characteristically marked egg which differs from the eggs of her conspecifics. By laying an egg with her own 'signature' the female is better able to recognize and then reject any parasitic eggs. The surprise then is that more species have not developed eggs marked with the signatures that would facilitate defense against intraspecific eggs.

Although there may well be other factors which render unmarked immaculate eggs advantageous to ducks, the fact is that duck eggs lack signatures. Does this mean they 'welcome' parasitism? While such tolerance is not universally the case (Semel *et al.* 1988), IBP could benefit some ducks. If hatching success is little affected by, or at least does not decrease with, the size of the clutch incubated, and if the chance that a hatchling will fledge increases with brood size, then it benefits a female for her eggs to be part of a large clutch. If she cannot lay the eggs herself, perhaps for physiological reasons, then an alternative is not to defend her clutch against parasites. Barrow's goldeneye (*Bucephala islandica*) females offer no such defense (Eadie and Fryxell 1992). A likely advantage to a duckling of being a member of large brood, or of a creche composed of the amalgamation of several broods, is that the chance of any one individual duckling falling foul of a predator falls. Exactly this dilution effect has been shown for ducklings of the common eider *Somateria mollissima* in Canada (Munro and Bédard 1977).

A similar dilution explanation has been used by Bertram (1992) to explain the remarkable nesting arrangements of the ostrich *Struthio camelus*. The first female to lay in a nest, scraped out by the territory-owning male, deposits around 11 eggs on alternate days. During this laying period of the so-called major female, up to five other females, the minor females, lay another 14 or so eggs in the nest. The major female steps aside to allow the minor females easy access to the nest. While some of the minor females' eggs are subsequently rolled out beyond the nest scrape by the major female, enough (around 8) are retained to reduce substantially the likelihood that a predator, say a jackal, will take one of the major female's eggs.

10.6 EVOLUTION OF INTERSPECIFIC BROOD PARASITISM

On current evidence, interspecific brood parasitism has evolved independently seven times in birds (Sorenson and Payne 2002, 2005): three times among cuckoos (order Cuculiformes), twice among Passeriformes, namely in the cowbirds (genus *Molothrus*, family Icteridae) and African brood parasitic finches (family Viduidae), once among the honeyguides (family Indicatoridae, order Piciformes) and once among waterfowl (black-headed duck *Heteronetta atricapilla*, order Anseriformes). Interestingly, interspecific brood parasitism evolved only once in precocial birds, although they show a much higher occurrence of intraspecific brood parasitism. This may imply that the benefits of brood parasitism are much higher in altricial birds where the costs of reproduction are much higher (Lyon and Eadie 1991). In five instances the evolution of interspecific brood parasitism is considered to be relatively old (the three instances in the Cuculiformes, the Viduidae and the Indicatoridae: > 10 million years, Davies 2000; Sorenson and Payne 2002) whereas the evolution of brood parasitism in the Icteridae and *H. atricapilla* is considered to be rather recent (< 5 million years, Sorenson and Payne 2002). This is not to be confused with subsequent radiation of brood parasitic taxa, as Sorenson *et al.* (2003, 2004) found that the extant vidnid species are less than five million years old, the radiation being most likely the result of colonization of new hosts rather than cospeciation.

One of the most intriguing questions is how brood parasitism evolved. As so often Darwin (1859) proposed a useful hypothesis, namely that interspecific brood parasites evolved from an ancestor with parental care. Hamilton and Orians (1965), Davies (2000) and Payne (2005) consider three potential avenues towards the evolution of interspecific brood parasitism.

Interspecific brood parasitism might have evolved from intraspecific brood parasitism (Payne 1977; Yamauchi 1995; Robert and Sorci 2001). Females that augment their fitness by laying eggs in nests of conspecifics will be selected for and indeed some cuckoo species are facultative intra- and interspecific brood parasites (Fleischer *et al.* 1985). Under strong nestling competition, interspecific brood parasitism will be selected over intraspecific brood parasitism (Robert and Sorci 2001). However, there is no close correlation between the occurrence of intraspecific brood parasitism and interspecific brood parasitism (Table 10.1) and it is therefore unlikely that intraspecific brood parasitism is a necessary precursor for the evolution of interspecific brood parasitism (Payne 2005).

A variant of this evolutionary scenario emphasizes the fact that cooperative breeding occurs in some cuckoo species. In cooperatively breeding species, there are ample opportunities to lay eggs parasitically and this might be a precursor of laying eggs in nests of other species. The potential importance of this precursor was emphasized by Hamilton (1964), but cooperative breeding is either rare or absent in the other taxa where interspecific brood parasitism evolved.

Finally, interspecific brood parasitism might have evolved directly from parental care (Cichon 1996). Potential evolutionary pathways might include nest takeover (Viduidae, Payne 2005), competition for nest sites leading to parasitism (Indicatoridae, Davies 2000) or parasitism of closely related species (Davies 2000; Sorenson *et al.* 2004). There is experimental evidence that parasitism on closely related species can produce healthy parasitic fledglings (Slagsvold 1998), but these were later shown to have lower recruitment and reproductive success, possibly due to false imprinting on their host species (Slagsvold and Hansen 2001). In conclusion, none of these pathways is entirely satisfactory in explaining the evolution of brood parasitism across all taxa and it might be that a unique combination of these pathways is required in each taxon.

What are the changes that occurred in ecology and life history when brood parasites evolved brood parasitism from an ancestor with parental care? Did these changes precede the evolution of brood parasitism or were they consequences? These questions have been tackled in comparative analyses. Krüger and Davies (2002) explained large amounts of variation of cuckoo reproductive strategies and showed that the transition from parental care to brood parasitism was accompanied by an increase in migratory behavior and breeding range size, but a decrease in egg size and a shift in diet towards smaller prey items (Table 10.2).

Table 10.2 Comparative analysis by independent contrasts, based on the phylogeny of Aragon *et al.* (1999), with reproductive strategy as the dependent variable (ranked from parental care to obligate brood parasite with a high fitness cost to the host species). A. Analysis of all contrasts ($n = 19$). The regression model is highly significant ($p < 0.001$). B. Analysis of contrasts among parasitic (facultative and obligate) taxa only ($n = 10$). The regression model is highly significant ($p = 0.001$). Modified after Krüger and Davies (2002).

A			
Variable	Slope	P	R ²
Egg size	Negative	0.002	0.449
Migration pattern	Positive	0.034	0.649
Breeding range size	Positive	0.002	0.747
Diet type	Negative	0.026	0.820

B			
Variable	Slope	P	R ²
Egg size	Negative	0.017	0.576
Population status	Negative	0.001	0.708
Diet type	Negative	0.010	0.884

Using a maximum likelihood approach (Pagel 1994), it was possible to construct the most likely evolutionary pathway between the presumed ancestral state and that displayed by modern brood parasitic species (Fig. 10.2). With the exception of egg size, changes in ecology were more likely to

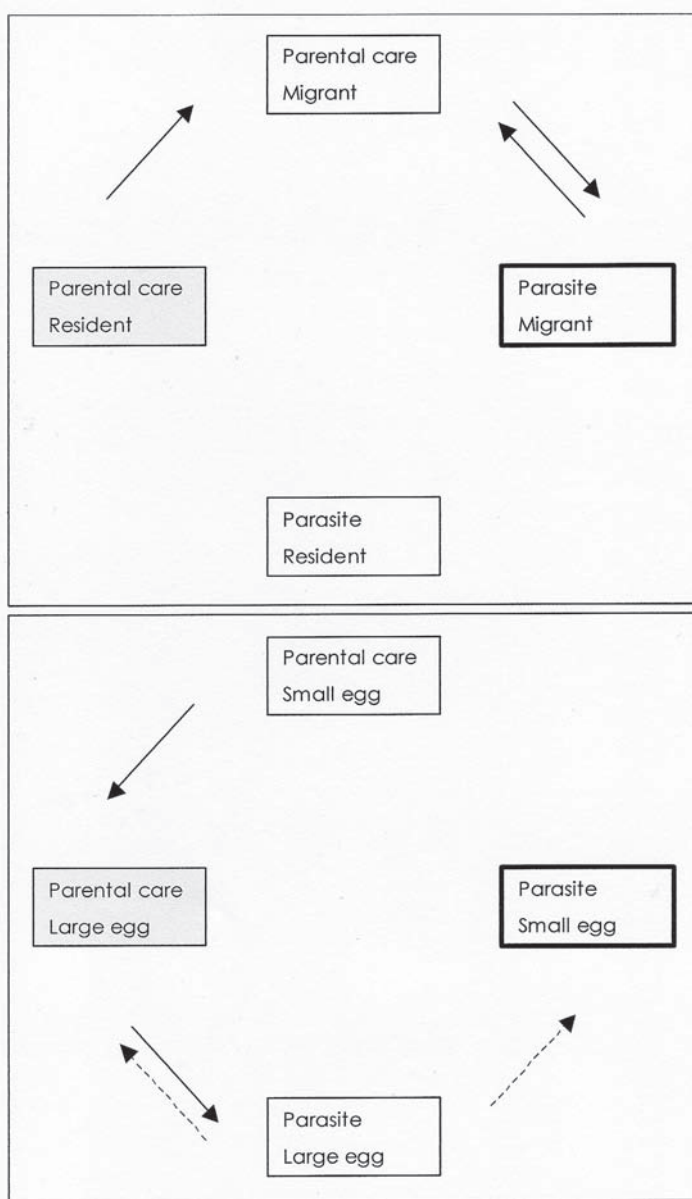


Fig. 10.2 Flow diagram of the most likely evolutionary pathways between cuckoo breeding strategies and migration pattern (top) and egg size (bottom). The presumed ancestral state is shaded in light grey, whereas the common current state in parasitic cuckoos is the boldly lined box. Solid arrows represent significant evolutionary pathways ($p < 0.05$) and dashed lines represent trends ($p < 0.1$). Modified after Krüger, O. and Davies, N. B. 2002. Proceedings of the Royal Society of London B 269: 375-381, Fig. 1.

precede the evolution of brood parasitism than to result from it. Hence, the evolution of brood parasitism in the Cuculidae is more likely to be a later adaptation, possibly reducing the cost of reproduction, whereas the reduction of egg size is a direct adaptation in the coevolutionary interaction with the host species. Similar to this, Mermoz and Ornelas (2004) found that parasitic *Molothrus* had thicker eggshells than non-parasitic species but did not differ in any other life history trait they examined.

10.7 TAXONOMIC OVERVIEW OF INTERSPECIFIC BROOD PARASITISM

Obligate interspecific brood parasitism is confined to four out of 28 taxonomic orders in birds (Davies 2000). Four of the seven brood parasitic taxa (the three cuculiform taxa and *Molothrus*) have received considerably more research effort than the other three. Because there are excellent recent reviews on Cuculidae and *Molothrus* (Ortega 1998; Rothstein and Robinson 1998; Payne 2005) and the other taxa are discussed in detail in Davies (2000), the taxonomic overview in this chapter will be very concise.

The most recent taxonomy of the Cuculidae recognizes 141 species (Payne 2005), of which 59 are brood parasites and 82 have parental care. They are found on all continents with the exception of Antarctica. They are an evolutionarily ancient taxon of birds, going back at least 60 million years (Rothstein and Robinson 1998). Among the brood parasitic species, a few parasitize their own species, some sometimes parasitize their own or other species and many are obligate brood parasites that rely entirely on host species for parental care. Obligate brood parasites are found in three monophyletic taxa: the Old World brood parasitic Cuculinae (52 species), the old world genus *Clamator* (4 species) and the New World brood parasitic genera *Tapera* and *Dromococcyx* (3 species). All brood parasitic cuckoos either evict or kill the host young, with the exception of *Clamator* cuckoos, where the young cuckoo is reared, at least initially, with the host young.

The brood parasitic species of the Icteridae of North and South America comprise a monophyletic taxon with five species of the genus *Molothrus* (Johnson and Lanyon 1999) nested within the family Icteridae (grackles and allies). They are much younger in evolutionary terms, at most 3-5 million years old (Rothstein *et al.* 2002). The parasitic *Molothrus* species do not evict host young from the nest, and hence host and parasitic young are raised together.

The second group of passerines to evolve interspecific brood parasitism is the African finches in the genera *Vidua* (10 species of indigobirds and 9 species of whydah) and *Anomalospiza* (1 species). Recent molecular phylogenies suggest that brood parasitism in this taxon originated maybe 20 million years ago (Sorenson and Payne 2001). However, the extant species of Viduidae are most likely comparatively recent (< 5 million years, Sorenson *et al.* 2004). Most species only parasitize a single host species and hence are the most specialized brood parasites (Davies 2000).

The 17 species of Indicatoridae from sub-Saharan Africa (15 species) and Asia (2 species) are included as a family with barbets (Lybiidae) and woodpeckers (Picidae) in the order Piciformes. Knowledge of the Indicatoridae is very poor compared to the aforementioned taxa, but they do not seem to be a recent evolutionary group (Sibley and Ahlquist 1990). A detailed phylogenetic study using DNA sequences is still awaited (Sorenson and Payne 2002). The final interspecific brood parasite is the Black duck (*Heteronetta atricapilla*) from South America. This species was only confirmed as an obligate brood parasite in 1968 (Weller 1968) and parasitizes other species of waterfowl and swamp-nesting birds. The species and brood parasitism are considered relatively recent (McCracken *et al.* 1999).

10.8 ADAPTATIONS AND COUNTER-ADAPTATIONS: BEFORE EGG LAYING

There is ample experimental evidence that brood parasites and host adaptations coevolve (Rothstein 1975b, 1990; Brooke and Davies 1988; Davies and Brooke 1989a,b; Moksnes *et al.* 1991a,b; Soler *et al.* 1994, 1998), but what happens before a brood parasitic egg is laid has not received that much attention.

There is now increasing evidence that individuals within and across host populations are not parasitized with equal probability (Lindholm 1999; Hauber *et al.* 2004). Recent evidence from radio-tracking and habitat selection studies indicates the importance of particular habitat features for female Common cuckoos *Cuculus canorus* (Teuschl *et al.* 1994; Nakamura and Miyazawa 1997; Honza *et al.* 2002; Vogl *et al.* 2002, 2004) and Brown-headed cowbirds *Molothrus ater* (Clotfelter 1998; Jensen and Cully 2005). In other words, parasitism is non-random. Such non-randomness has been documented for nest sites of hosts; Øien *et al.* (1996), Moskat and Honza (2000) and Clotfelter (1998) found that host nests closer to a potential perches such as trees and those more obvious to a human observer were more likely to be parasitized and Hauber (2001) showed that Phoebe *Sayornis phoebe* nests were more likely to be parasitized if located under eaves than under bridges. Hauber *et al.* (2004) showed that this non-randomness in parasitism can constrain the evolution of host defenses and, all else being equal, parasitic females should select host parents of high quality. Indeed Soler *et al.* (1995) found evidence that Great spotted cuckoos *Clamator glandarius* prefer to parasitize large nests of their Magpie *Pica pica* hosts, a large nest apparently indicating high parental quality. Brooker and Brooker (1996) reported that young and/or inexperienced splendid fairy-wrens *Malurus splendens* were most likely to be parasitized by the Horsfield's bronze cuckoo *Chrysococcyx basalis*, demonstrating non-randomness with regard to age and/or experience of the host. However, Payne and Payne (1998) could not detect an effect of host female age in indigo buntings *Passerina cyanea* on the probability of parasitism by *M. ater*.

This poses the question whether this non-randomness results from parasite behavior or defense behavior by the host? A few studies have tried to determine what cues are used by brood parasites to locate host nests. The two commonly stated hypotheses are the nesting-exposure hypothesis and the nesting-cue hypothesis (Robertson and Norman 1976; Gill *et al.* 1997; Clotfelter 1998). Parasites either preferentially use conspicuous host nests or those where the hosts show conspicuous behavior. As mentioned above, there is some evidence for the nesting-exposure hypothesis but when Gill *et al.* (1997) and Clotfelter (1998) tested the nesting-cue hypothesis in *Molothrus ater* hosts, they did not find any support.

The key counter-adaptation of hosts before a parasitic egg is laid is aggression towards the parasitic female (Moksnes *et al.* 1991a; Sealy *et al.* 1998). Indeed unsuitable host species have been shown to react less aggressively towards a *Cuculus canorus* dummy than suitable host species (Moksnes *et al.* 1991a) and hosts of *Molothrus ater* show increasing aggression with increasing parasitism rate (Robertson and Norman 1976). This aggressive behavior is a specific response to parasitism: the response to predators differs significantly (Duckworth 1991). Aggression also ceases when the host young have fledged or late in the season (Davies *et al.* 2003).

10.9 ADAPTATIONS AND COUNTER-ADAPTATIONS: THE EGG STAGE

The overall scheme of coevolution in parasite-host systems is illustrated in Fig. 10.3, the coevolutionary stages are well illustrated by egg coloration and egg size as we shall now discuss.

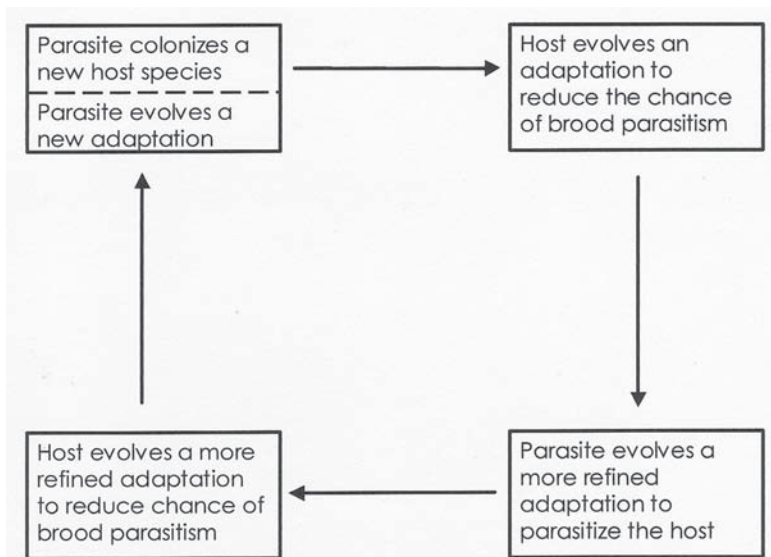


Fig. 10.3 Scheme of the coevolutionary arms race between a brood parasite and its host. Original.

Brood parasitism imposes costs on hosts at the egg stage: in many parasitic species the laying female removes a host egg when she lays (Payne 2005), and even in those species where no host egg is removed, a reduction in host clutch size has been documented through eggs being punctured by the parasitic female (Massoni and Reboreda 1998, 2002; Hoover 2003) or cracked by the parasitic egg (Davies 2000).

Given the selection pressure on hosts to reject parasitic eggs from their nests, it comes as no surprise that a number of counter-adaptations has been documented at the egg stage. There is some evidence that hosts learn to recognize their eggs and base their rejection behavior on this information (Victoria 1972; Lotem *et al.* 1992). Some host species subsequently desert the entire nest if they are parasitized (Hill and Sealy 1994), some puncture the parasitic egg with their beak and throw it out of the nest or roll the parasitic egg out of the nest (Davies 2000; Lorenzana and Sealy 2001), and others bury the parasitic egg and their own eggs under a new layer of nest material (Sealy 1995). On a larger scale, the duration of sympatry between parasite and host can explain significant amounts of variation in egg rejection behavior, with longer times of sympatry being associated with higher rejection behavior (Rothstein 1975b; Peer and Sealy 2004). Along these lines, gene flow between unparasitized and parasitized host populations also explains a lot of variation in egg rejection behavior (Soler *et al.* 1999; Røskaft *et al.* 2002a).

Size also matters for parasitic eggs, because host species might use differences in either coloration or size to detect a parasitic egg (Davies and Brooke 1988). Good evidence for the importance of egg size as an adaptation to brood parasitism comes from a study on the lesser cuckoo *Cuculus poliocephalus* by Marchetti (2000). *C. poliocephalus* parasitizes Tickell's leaf warbler *Phylloscopus affinis*, but not the closely related Hume's yellow-browed leaf warbler *Phylloscopus humei*. Experiments showed that *P. humei* rejected eggs on the basis of relative size; model eggs 75% larger in size than host eggs (but still smaller than the real cuckoo egg) were rejected. These species build domed nests and the dark environment might preclude egg coloration from being a reliable clue. The response of the host puts this cuckoo species under selection pressure to evolve a smaller egg, which was identified as a major adaptation to brood parasitism in general by Payne (1974) and Krüger and Davies (2002, 2004).

The evolution of a small egg could be achieved through a reduction in body size (there is a strong allometric relationship between body size and egg size in birds in general and cuckoos in particular) or through the evolution of an unusually small egg in cuckoos. Darwin (1859) commented on the small egg of *C. canorus*, and Payne (1974) showed that brood parasitic cuckoos lay smaller eggs than cuckoos of the same size with parental care. Krüger and Davies (2004) looked at two of the most speciose cuckoo genera, to test which mechanism explained the closer size matching of cuckoo and host eggs in *Chrysococcyx* compared to *Cuculus* (Fig. 10.4). *Chrysococcyx* species are relatively small and parasitize dome-nesting host species, whereas the great

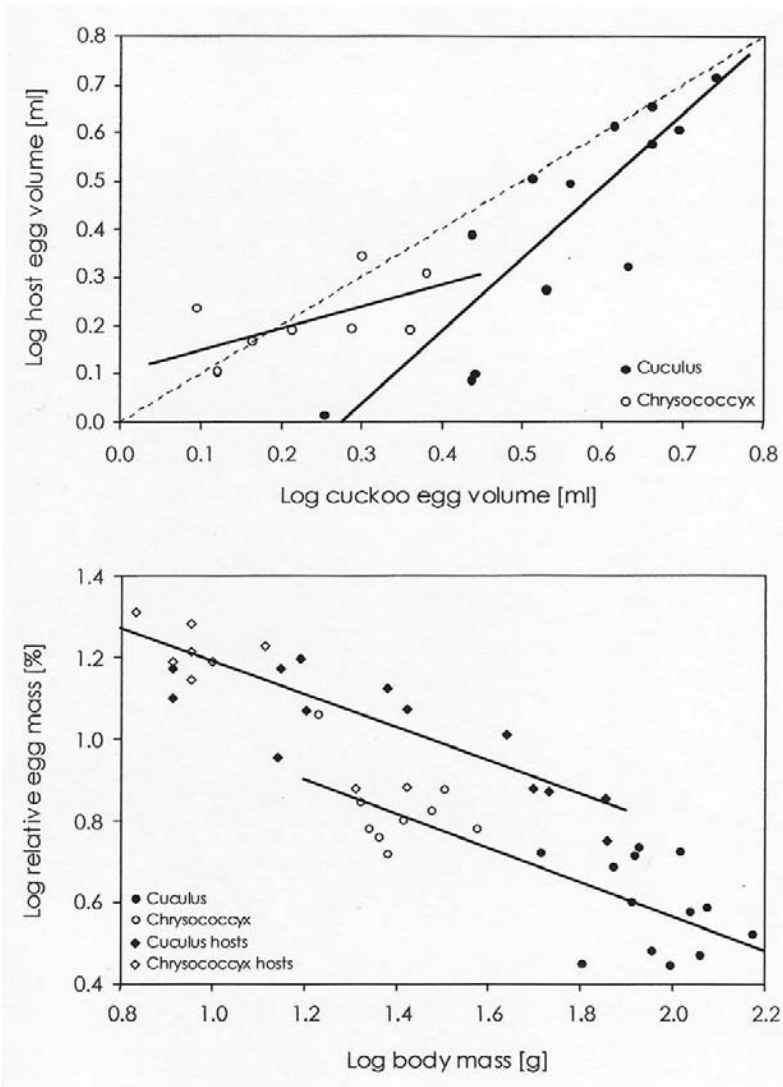


Fig. 10.4 Top: Comparison of host egg volume and cuckoo egg volume for *Chrysococcyx* species ($y = 0.455x + 0.099$, $r^2 = 0.371$, $F_{1,7} = 4.125$, $p = 0.082$) and *Cuculus* species ($y = 1.490x - 0.415$, $r^2 = 0.742$, $F_{1,11} = 31.609$, $p < 0.001$). Slopes differ significantly ($t_{18} = 5.329$, $p < 0.001$). The dashed line is $y = x$. Bottom: Relationship between body mass and egg mass relative to body mass for *Chrysococcyx* and *Cuculus* cuckoos ($y = -0.408x + 1.395$, $r^2 = 0.614$, $F_{1,20} = 31.814$, $p < 0.001$) and their hosts ($y = -0.408x + 1.582$, $r^2 = 0.713$, $F_{1,20} = 49.796$, $p < 0.001$). Slopes do not differ significantly between the two ($t_{40} = 0.067$, ns). Modified after Krüger, O. and Davies, N. B. 2004. Behavioral Ecology 15: 210-218, Fig. 5 and 7.

majority of *Cuculus* species are larger and parasitize cup-nesting host species. The better size matching between parasitic and host egg in *Chrysococcyx* is not achieved through an unusually small egg, but through reduced body size (Fig. 10.4) and this might reflect a selection pressure to be small in order to enter the domed nests of the hosts to lay.

Apart from egg size, eggshell strength is another important trait. Parasitic cuckoos lay eggs of higher eggshell strength and/or eggshell density than nesting cuckoos of the same body size (Brooker and Brooker 1991; Picman and Pribil 1997, but see Payne 2005). In general, brood parasites lay eggs that are thicker shelled (Picman 1989; Picman and Pribil 1997; Mikhailov 1997) which facilitates rapid laying by parasitic females and makes egg puncturing by hosts more difficult.

However, by far the best-studied adaptation of brood parasites to egg-rejection of hosts is egg mimicry (Davies 2000; Payne 2005). In some brood parasites such as Indicatoridae and Viduidae, similarities between parasitic egg and host egg are best explained by common ancestry rather than coevolution (Davies 2000, see also Grim 2005), but the selection pressure that hosts impose on brood parasites to lay mimetic eggs has been recognized for almost a century (Baker 1913) and there is good evidence that hosts accept mimetic eggs while they reject non-mimetic ones (Brooke and Davies 1988; Davies and Brooke 1988; Lotem *et al.* 1995). Whereas the generalist brood parasitic *Molothrus* species do not exhibit egg mimicry for the great majority of their hosts, many Cuculidae species lay mimetic eggs (Fig. 10.8C), sometimes indistinguishable from the host egg by the human eye (Langmore *et al.* 2003) and even a good match for the host egg in the UV-spectrum (Cherry and Bennett 2001; Langmore *et al.* 2003). But the coevolutionary process does not necessarily stop there. Brood parasites using more than one host species have been shown to evolve host-specific egg-morphs (females laying a particular egg-morph being referred to as a gens), with genes coding for the egg-pattern being most likely located on the female-specific W-chromosome (Gibbs *et al.* 2000), while hosts have been shown to evolve larger inter-clutch variation but smaller intra-clutch variation (Stokke *et al.* 1999, 2002) which renders the evolution of egg mimicry much more difficult and might select for the evolution of egg polymorphism in the host (Takasu 2003).

As astonishing as the variety of adaptations and counter-adaptations at the egg stage is its apparent lack in some parasite-host systems. Although it is estimated from historical records that *Cuculus canorus* has parasitized Dunnocks (*Prunella modularis*) for at least 600 years (Davies and Brooke 1989a), they never reject an egg, even one that looks completely different from their own, despite the obvious fitness cost of brood parasitism. Similar situations have been documented for the Red-chested cuckoo (*Cuculus solitarius*) the Jacobin cuckoo *Clamator jacobinus* (Fig. 10.8D) and many hosts of *M. ater*, despite large differences in both coloration and size (Liversidge 1970; Ortega 1998; Davies 2000). If parasite-host systems represent the coevolutionary process, these situations need an explanation. Under which

circumstances could it not be the best option to reject a parasitic egg? Even deserting the brood leads to another chance to breed, either in the current or next season, whereas raising a cuckoo chick not only reduces reproductive success of the parents to zero, but might reduce the chance of future reproductive success through reduced survival. There is good evidence that rejection of parasitic eggs carries a twofold cost. First, hosts commonly damage their own eggs in the process of removing a cuckoo egg (Davies and Brooke 1988; Marchetti 1992) and secondly, they sometimes make recognition errors and eject one or more of their own eggs from the clutch, whether they have been parasitized or not (Davies and Brooke 1988; Marchetti 1992; Lotem *et al.* 1995). An intriguing third cost of rejection was suggested by Zahavi (1979): where the hosts reject a parasitic egg, the parasite destroys the nest in retaliation. However, the study by Soler *et al.* (1995) on the great spotted cuckoo *C. glandarius* remains the only evidence to date for such an avian Mafia.

Given that both egg rejection and acceptance have costs and benefits, an optimality approach can be applied to work out a threshold frequency of brood parasitism above which egg rejection results in higher reproductive success and below which egg acceptance is favored. Such an approach was used by Davies *et al.* (1996) and showed a threshold frequency of 19% when *C. canorus* were parasitizing Reed warblers (*Acrocephalus scirpaceus*) at one site. The general approach is illustrated in Fig. 10.5 and can also be used to look at the population dynamics of a parasite-host system (Takasu *et al.* 1993).

10.10 ADAPTATIONS AND COUNTER-ADAPTATIONS: THE CHICK STAGE

Even before the parasitic chick hatches, adaptations increase its competitive ability. Rapid embryonic development has been observed in both *Molothrus* and Cuculinae species (Friedmann 1929, Liversidge 1961) and McMaster and Sealy (1998) showed that *M. ater* eggs achieve a shorter incubation period than hosts eggs due to more efficient incubation by the host and worse incubation of the host eggs. Incubation periods shorter than those of hosts are also known for many other parasitic species within the Cuculinae and Viduidae (Payne 2005). To hatch from an egg with a thicker shell compared to host eggs requires more time and effort, as Honza *et al.* (2001) documented for *Cuculus canorus* chicks.

Soon after hatching, parasitic chicks of most cuculiform species and the Indicatoridae eliminate competition with host chicks through eviction or killing (Davies 2000; Payne 2005). In contrast, chicks of a few cuculiform species, *Molothrus* and Viduidae are commonly raised together with the host chicks. In these species, adaptations have enabled the parasitic chick to compete successfully with the host chicks. There is good evidence that both *M. ater* and *Clamator glandarius* chicks are preferentially fed by their host parents (Redondo 1993; Dearborn 1998). This preferential treatment can be achieved through the parasitic chick being larger (Liversidge 1970; Dearborn

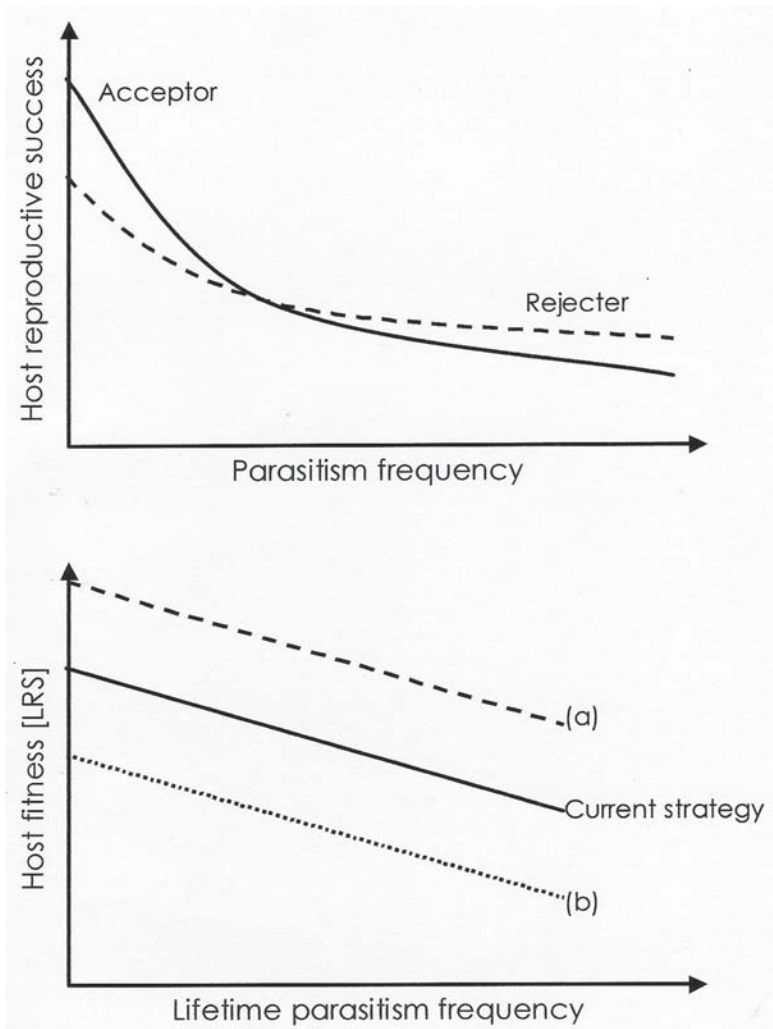


Fig. 10.5 Relationship between parasitism frequency and host reproductive success for acceptor and rejecter strategies (top). The model assumes that there are costs of acceptance and also costs of rejecting a parasitic egg. In the absence of brood parasitism, acceptors have the highest reproductive success but at high parasitism frequencies the costs of acceptance are higher than the costs of rejecting and rejecters have a higher reproductive success. Schematic relationship between lifetime parasitism frequency and host fitness (bottom). The current strategy defines a given degree of egg rejection which can vary from zero to one. If a new strategy would have higher fitness (a), this would point towards evolutionary lag in the current strategy but if a new strategy would have lower fitness (b), this would point towards evolutionary equilibrium in the current strategy. Top panel modified after Takasu (1998) and Winfree (1999).

1998), providing extra stimuli that facilitate preferential treatment (Fig. 10.8E and F; Soler *et al.* 1995, but see Lichtenstein and Sealy 1998) or by begging selfishly and dishonestly (Lichtenstein 2001, but see Hauber and Ramsey 2003). The question arises why, given the absence of kin selection benefits between parasitic and host chicks, do parasites in these species not obligatorily outcompete host chicks? Kilner *et al.* (2004) provided a neat explanation for this in *M. ater*: chicks raised together with host chicks grew faster than chicks raised without nestmates, hence parasitic chicks might use host chicks to procure resources. This discovery, however, raises the question how parasitic chicks of evicting species receive enough parental care from their host parents. Davies *et al.* (1998) and Kilner *et al.* (1999) showed that a single *C. canorus* chick has unusually rapid begging calls that sound like an entire brood of four *Acrocephalus scirpaceus* chicks, and that this supernormal vocal stimulus compensates for a subnormal visual stimulus of one gape. This ensures that the parasitic chick gets sufficient food and similar observations have been made in chicks of Indicatoridae (Fry 1974). Selfish or exaggerated begging might come at a cost and indeed Dearborn (1999) reported that begging calls at indigo bunting *Passerina cyanea* nests parasitized by *M. ater* were louder than at unparasitized nests and that parasitized nests had a higher predation rate, which has also been observed in Viduidae (Payne 2005). Recent evidence suggests that begging calls and especially the response to parental alarm calls can be host-specific and differ between gentes of *C. canorus* (Butchart *et al.* 2003; Davies *et al.* 2006), hence fine-tuning into host communication systems might be even more elaborate than previously realized.

Interestingly, despite subtle adjustments of begging behavior, visual chick mimicry is essentially absent in brood parasites with the exception of the screaming cowbird *Molothrus rufoaxillaris* and the Viduidae (Davies 2000). In the Viduidae, the elaborate and colorful mouth markings in the hosts are mimicked by the parasitic chick in great detail. While common ancestry is thought to be the starting point for the mimicry, the host-specificity of the mouth marking can only be explained through subsequent parasite-host coevolution (Sorenson and Payne 2002). But the chick mimicry does not completely preclude the colonization of new host species (Payne *et al.* 2001) and there are hosts with non-mimetic parasitic chicks.

A previously unknown adaptation in a cuckoo chick comes from a study of the Horsfield's hawk-cuckoo *Hierococcyx hyperythrus* in Japan. Tanaka and Ueda (2005) discovered that, to manipulate its foster parents, the young cuckoo has a vivid yellow skin patch on each wing-bend that matches its own gape color. The young cuckoo flashes these yellow skin patches at the host parent to stimulate feeding and indeed host parents sometimes try to feed the wing patch. Experimentally hiding this stimulus by paint reduces the feeding rate by the host, demonstrating the adaptive value of the skin patch.

Hosts are not completely defenseless at the chick stage. An example of how hosts can retaliate against a parasitic chick comes from Australia, where

Horsfield's bronze cuckoo (*Chrysococcyx basalis*) parasitizes the Superb fairy wren (*Malurus cyaneus*). The cuckoo lays a highly mimetic egg and hosts accept it. However, hosts deserted 11 out of 29 parasitic chicks, sentencing them to death through starvation or cold (Langmore *et al.* 2003). This is partly a response to parasitic chicks, because single host chicks were abandoned at a lower rate. This behavior shifts the arms race to the chick stage, but the mechanism behind chick recognition is unclear. While hosts can learn the appearance of the eggs through imprinting on their first clutch (Lotem *et al.* 1995), imprinting on the first chick has been proposed to be highly maladaptive. If parasitized in their first breeding attempt, parents would then reject all their subsequent young (Lotem 1993). However, Langmore *et al.* (2003) did not find evidence for this: parents that accepted a parasitic chick did not abandon their own chicks in subsequent breeding attempts. Another possible means of defense against parasitism at the chick stage has been suggested by Grim *et al.* (2003) who found that, in some cases, *Acrocephalus scirpaceus* parents stopped feeding a *Cuculus canorus* chick after the cuckoo needed more food than an entire unparasitized brood. If parents were using the amount of parental care required as a discriminating mechanism, no learning or imprinting would need to be invoked.

Finally, the choice of a host species also affects offspring quality in brood parasites, as has been demonstrated by Kleven *et al.* (1999). *Cuculus canorus* of the *Acrocephalus scirpaceus* gens also parasitize the Great reed warbler (*A. arundinaceus*) at a study site in the Czech Republic, and cuckoo chicks raised by *A. arundinaceus* grew at a faster rate and fledged significantly heavier than cuckoo chicks raised by *A. scirpaceus*. In a further study, Kleven *et al.* (2004) showed that both hatching success of cuckoo eggs and fledging success differed significantly between four sympatric *Acrocephalus* warbler hosts.

Apart from the quality of parental care received, the host species in which parasites are raised has important repercussions for the adult parasite. In the Viduidae, imprinting on host song is crucial for parasitic males' later mating success (Payne *et al.* 2000). While Cuculinae species must have an innate basis for the development of their song (Davies 2000), habitat imprinting has been suggested to be of major importance for finding suitable habitats and hosts in *Cuculus canorus* (Teuschl *et al.* 1998).

10.11 COEVOLUTIONARY ARMS RACES: OUTCOMES

Two main hypotheses have emerged which try to explain the evolutionary state of parasite-host systems in general and the lack of host defenses in some host species in particular (Davies and Brooke 1989b). The *evolutionary lag hypothesis* proposes that it would be advantageous for hosts to counteract brood parasitism but they do not, either because there has been insufficient time for the defense to spread through the host species population or because hosts might lack the genetic variation to evolve a defense against brood parasitism (Rothstein 1975b). The *evolutionary equilibrium hypothesis* proposes that the costs of brood parasitism do not always exceed the costs of rejection

and, hence, under some scenarios it is adaptive for a host to accept brood parasitism. In the case of *Prunella modularis* accepting any *Cuculus canorus* egg in its nest, the evolutionary lag hypothesis proposes that *P. modularis* simply lacks the necessary genetic variation or there has been insufficient time for egg rejection to evolve and spread, whereas the evolutionary equilibrium hypothesis proposes that the costs of egg rejection are higher than the cost of brood parasitism, hence *P. modularis* does better to accept the egg of *C. canorus*. In theory, one could differentiate between the two hypotheses by looking at the current strategy in a population (egg acceptance or egg rejection) and at the lifetime fitness payoff of an alternative strategy (Fig. 10.5). If the fitness of the alternative strategy was higher than the fitness of the current strategy, this would support the evolutionary lag hypothesis. However, if the fitness of the alternative strategy was lower than the current strategy, this would support the evolutionary equilibrium hypothesis. This is easier said than done, given that one can hardly turn an acceptor into a rejecter and hence measure the lifetime cost of egg rejection. Even documenting a lack of genetic variation in a host population with regard to egg acceptance does not provide conclusive evidence for the evolutionary lag hypothesis as suggested by Winfree (1999). Under strong selection pressure for egg acceptance, this trait would be expected to spread to fixation and no genetic variation should be detectable, even if evolutionary equilibrium operates. Rejecting hosts could, however, be experimentally turned into acceptors by adding a parasitic chick to their nest (Winfree 1999), because hosts do not reject chicks (but see Langmore *et al.* 2003). Another, potentially more fruitful, approach is to combine detailed measurements of the benefits and costs of acceptance with modeling studies to produce likelihood estimates for the evolution of egg rejection and hence an indirect test of the two hypotheses.

The long-term outcomes of cuckoo-host interactions can be grouped into three cases: continued exploitation of hosts that do not show any defense; oscillatory systems, where brood parasitism frequency and host defense levels fluctuate around an evolutionary equilibrium and where fitness pay-offs of egg acceptance and egg rejection are equal; and systems where the host seems to have evolved counter-adaptations that preclude successful parasitism.

The *Cuculus canorus* – *Prunella modularis* system would be an example of continued exploitation with no host defenses and some hosts of *Molothrus ater* do not exhibit defenses despite high parasitism rates (Ortega 1998). One can imagine host populations being stable despite heavy cowbird parasitism, because cowbirds do not impose such a high fitness cost but what about those parasites where a successful parasitism event reduces host reproductive success to zero? Barabas *et al.* (2004) looked at some *Acrocephalus arundinaceus* populations in Hungary, where parasitism by *C. canorus* has been extraordinarily high at 50–66% for several decades. They showed that such host populations can only be maintained in a metapopulation framework with immigration from other, less parasitized areas. But continued exploitation of hosts can have important conservation implications in rare

and localized hosts (Rothstein and Robinson 1994; Arcese *et al.* 1996; Trine *et al.* 1998). The effect of parasitism by *M. ater*, for example, is not restricted to reducing the reproductive success of host, but can skew host offspring sex-ratios (Zanette *et al.* 2005) and affect host population growth rate significantly (Smith *et al.* 2002).

There is also evidence that some parasite-host systems are in a dynamic state of oscillation. For example, the *Cuculus canorus*–*Acrocephalus scirpaceus* system shows dynamic behavior at least in one location. Brooke *et al.* (1998) documented a decline in egg rejection behavior in line with declining levels of brood parasitism, and the decline was so rapid that it was most likely due, not to genetic changes in the host population, but to behavioral flexibility.

Some species, which have very likely been cuckoo hosts in the past, have evolved seemingly watertight defenses against brood parasitism. Hume's leaf warbler *Phylloscopus humei* from India studied by Marchetti (2000) showed a very high rejection rate of the larger parasitic eggs and it seems very unlikely that the large parasite could ever evolve an egg small enough to mimic the tiny host's egg. Another example has been documented from Hungary, where the red-backed shrike *Lanius collurio* was parasitized by *Cuculus canorus* regularly until the late 1960s, but no parasitism has been recorded since. Lovaszi and Moskat (2004) found that 93% of real cuckoo eggs were rejected, so it seems that the host has won. Honza *et al.* (2004) regard the blackcap *Sylvia atricapilla* as another winner in the arms race with *C. canorus*. Throughout Europe, they reject parasitic eggs with almost 100% frequency and Honza *et al.* (2004) documented very low intra-clutch variation in egg appearance, but high inter-clutch variation. The large inter-clutch variation severely constrains egg-mimicry, while the low intra-clutch variation permits effective egg discrimination. Comparative evidence supports this as an effective mechanism against brood parasitism (Stokke *et al.* 2002). Under these scenarios, the cuckoo gens that parasitized a particular host species either becomes extinct or successfully switches host species. The best evidence that brood parasites can switch hosts comes from Japan, where *C. canorus* started parasitizing azure-winged magpies *Cyanopica cyana* only in 1956, with current parasitism rates as high as 60% (Nakamura *et al.* 1998). Additional, indirect evidence for host switching comes from the *C. solitarius* — Cape robin *Cossypha caffra* system where there is a lack of egg mimicry, but egg acceptance. However, the *C. solitarius* egg is an excellent match for three other robin species that are only rarely parasitized (Davies 2000) and it is tantalising to suggest that egg mimicry for rarely-used hosts might be a sign of the ghost of evolution past. That is, *C. solitarius* once parasitized these hosts, but their egg rejection behavior now constrains this and a new cuckoo gens has evolved, parasitizing the naïve *C. caffra*.

10.12 POTENTIAL FUTURE RESEARCH AVENUES

Brood parasites and their hosts provide a model system for the coevolutionary process (Rothstein 1990), but they are also very interesting models for the

evolution of mating and life history strategies. On current evidence, female gentes of *C. canorus* represent alternative reproductive strategies, i.e. they are true genetic alternatives rather than conditional tactics (Gross 1996). Further genetic data are needed to look at mating systems and scope for sexual conflict in parasitic species (see Hauber and Dearborn (2003) for a recent review on genetic studies of cuckoo mating systems). Female reproductive success would benefit from better adaptation to the particular host species, but the cross-mating between gentes compromises this. Hence, this is a scenario where the benefits of polygyny to males are higher than the benefits of a better adaptation to a particular host species. This conflict between the sexes could prove to be a fruitful target for modeling efforts, first to look at the rate of cross-mating necessary by males to prevent speciation events and, secondly, to examine the dynamic game between hosts, female and male *C. canorus* in terms of adaptation. However, there is also good evidence that monogamy among females is very widespread (Martinez *et al.* 1998; Marchetti *et al.* 1998; Alderson *et al.* 1999; Woolfenden *et al.* 2002; Strausberger and Ashley 2003). This demands an explanation, since presumably males would benefit from multiple mates and females from the potential genetic benefits of mating with several males.

Within the modeling realm, more effort could be devoted to refining current models of the costs and benefits of egg rejection or acceptance. There is good evidence that the risk of being parasitized is not equal between individuals of a host population and neither is it equal across an individual host's lifespan (Lotem *et al.* 1992; Brooker and Brooker 1996; Øien *et al.* 1996; Grim 2002). For the sake of simplicity these relationships are not considered in models or analyses of costs and benefits of parasite-host coevolution (Takasu *et al.* 1993; Brooke *et al.* 1998; Servedio and Lande 2003). However, the cost of brood parasitism to a host is very likely to be non-linear over the host's lifespan. Reproductive success in birds is commonly related to age in a non-linear fashion (Sæther 1990; Forslund and Pärt 1995; Krüger and Lindström 2001; Reid *et al.* 2003). Hence, from a lifetime reproductive success perspective, being parasitised in the first or last breeding attempt is likely to be less costly than being parasitised during the prime years. Many host species are reasonably long-lived and hence this non-linearity should be included in quantitative models of the costs of brood parasitism. This, however, also means that brood parasites should selectively parasitize prime-aged hosts.

Another trait that is commonly assumed constant is parental host quality, which affects the probability of fledging for the cuckoo chick. Parasitism is non-random and it would be interesting to see whether cuckoo females select hosts for their parental quality and how they assess this (see Soler *et al.* 1995 for one example). The effect of brood parasitism on the life history strategy of the host species could merit further research. For example, Hauber (2003) used a comparative approach to document that hosts of *Molothrus ater* have reduced clutch sizes, which is exactly what life history theory predicts under increased juvenile mortality in host species. This approach could be complemented by long-term individual-based studies to look at the true fitness

effects of brood parasitism by measuring lifetime reproductive success (LRS) for host individuals. Brooker and Brooker (1996) achieved this for *Malurus cyaneus*, host of *Chalcites basalis*. They reported that, despite obvious costs in any one breeding attempt, the lifetime reproductive success of those individuals that were never parasitized was not higher than the LRS of individuals that were parasitized once or more than once. This, however, is likely to be an effect of phenotypic correlations: high quality females were able to compensate for brood parasitism, despite it being costly. In addition, they found that brood parasitism did not lower subsequent survival probability; hence, the costs were restricted to lower reproductive success (see also Payne and Payne 1998 for a similar result in a host of *M. ater*). Given the non-randomness of parasitism that they document, this correlational study should be backed-up by experimental approaches to test whether brood parasitism at a certain age of an individual can have a fitness consequence. This experimental approach could be viewed as a perturbation analysis of a matrix analysis to test whether the reduction of a matrix element (here reproductive success) has fitness consequences (Caswell 2001). More fitness data are also needed to analyze which factors in the absence of brood parasitism explain differences in individual fitness within a host population.

Although much research has been devoted to begging behavior of parasitic versus host chicks (Kilner *et al.* 1999; Butchart *et al.* 2003), much more needs to be done. For example, Kilner *et al.* (2004) recently showed that *Molothrus ater* chicks raised with host chicks grow faster than if they are raised alone, so they use host chicks to procure more resources. It would be interesting to know what happens between parasitic and host chicks for the non-ejecting Cuculinae species and the Viduidae. This should include further research on the interplay between hormones and begging behavior. While two studies have shown that brood parasites do not deposit more testosterone into their eggs than their hosts (Hauber and Pilz 2003; Torök *et al.* 2004), Groothuis and Ros (2005) showed that testosterone reduces begging and so there is still ample scope to test whether hormones play a part in the superior competitive ability of non-evicting brood parasites. It might also be useful to use comparative approaches to generalize how different parasitic species exploit their hosts in terms of begging behavior. A further aspect of begging behavior of parasites that deserves attention is host-specificity. First evidence is emerging that *Cuculus canorus* gentes also have host-specific communication strategies (Davies *et al.* 2006) and the evolution of this might be elucidated by looking at other cuckoo species where gentes are present.

One final field that might deserve more attention could be the interactions between predation risk and parasitism risk. Brood parasitism can be viewed as a form of nest predation given that the host's reproductive success of that breeding attempt is regularly (ejecting Cuculiformes and Indicatoridae), often (non-ejecting Cuculiformes) or seldom (*Molothrus* and Viduidae) reduced to zero. However, brood parasites share a common interest with their hosts in that they benefit if the nest is not found by a predator after they have laid an

egg. Host species are under selection pressure to find nest sites and build nests in a way that minimizes the risk of both predation and parasitism simultaneously. Two scenarios are conceivable (Fig. 10.6): if a trait of a host species affects predation and parasitism risk in the same way, strong directional selection on the trait would be expected. However, if an increasing trait value decreases predation risk but increases parasitism risk, balancing selection occurs with the optimal trait value being determined by the fitness

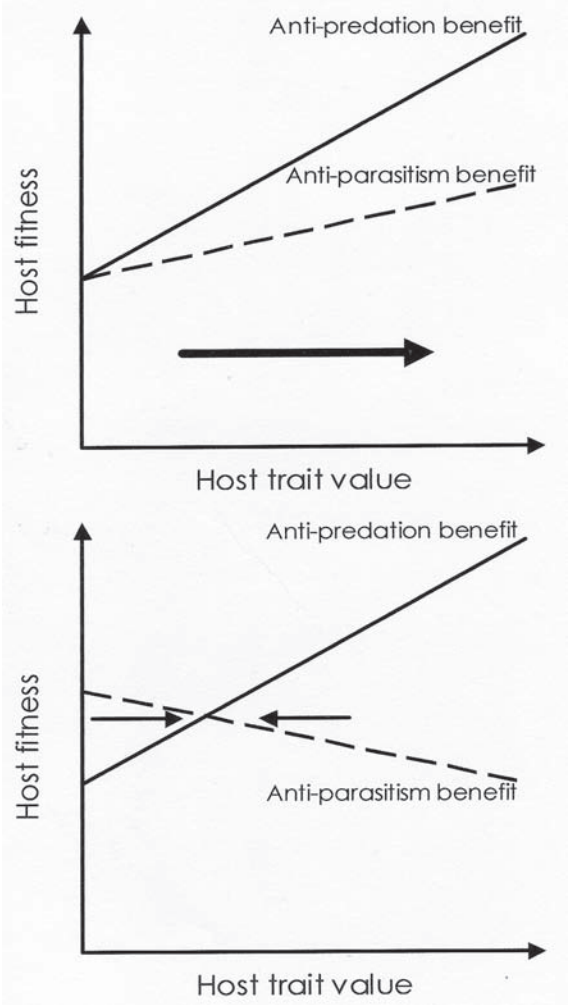


Fig. 10.6 Scheme showing the relationship between a host trait and its fitness value for both predation and parasitism risk. If a trait affects host fitness similarly under both predation and parasitism, the resulting selection pressure will be directional (top), but if predation and parasitism risk are affected in opposite directions, balancing selection pressure is the result (bottom). Original.

slopes for predation and parasitism and their respective frequency. Such a trade-off between the effects of parasitism and nest predation has recently been documented for a host of *M. ater* (Tewksbury *et al.* 2002). There is also evidence for complex trade-offs in the host-parasite system between the Jacobin cuckoo (*Clamator jacobinus*) and Cape bulbul (*Pycnonotus capensis*) (Krüger 2004, Fig. 10.7). By measuring variables describing nest site selection and nest architecture, 70% of nests can *a priori* be correctly assigned into the categories successful, parasitized or predated, so both predation and

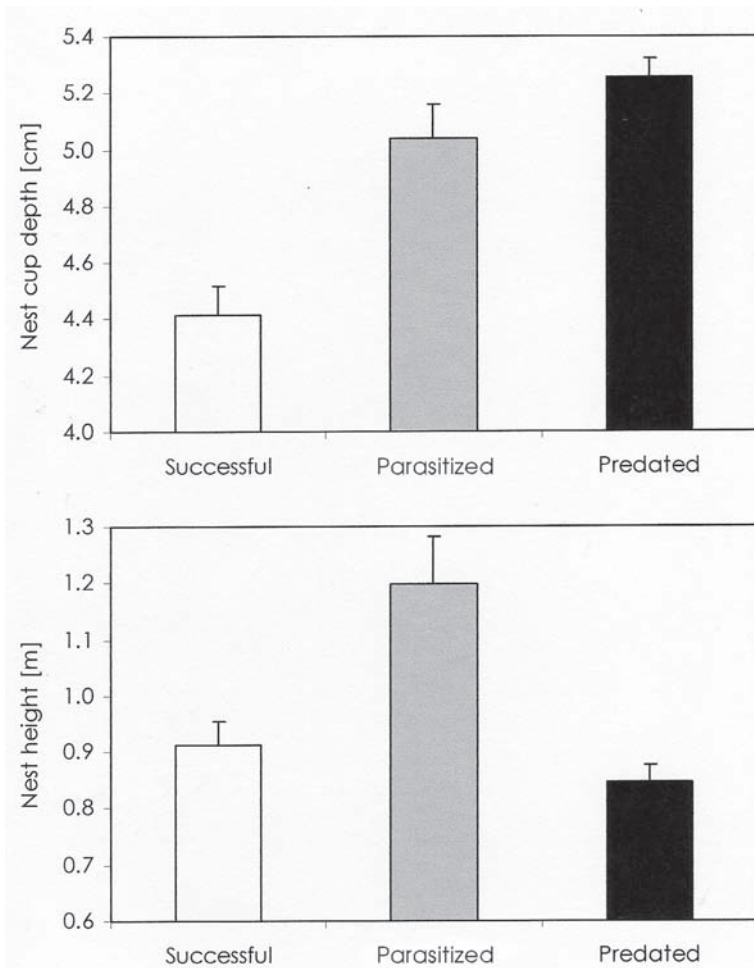


Fig. 10.7 Differences between successful (fledging at least one host chick), parasitized and predated nests of the Cape bulbul *Pycnonotus capensis* from a study in South Africa (Krüger 2004), documenting a directional selection pressure on nest architecture such as cup depth (top), but a balancing selection pressure on nest height (bottom) Differences in both cup depth ($F_{2,159} = 23.008$, $p < 0.001$) and nest height ($F_{2,159} = 9.760$, $p < 0.001$) are highly significant. Original.



Fig. 10.8 **A.** Incubating Moorhen (*Gallinula chloropus*), **B.** brood of Barrow's goldeneye ducks (*Bucephala islandica*) with color-marked chicks originating from different females, **C.** Reed warbler (*Acrocephalus scirpaceus*) clutch with a Common cuckoo (*Cuculus canorus*) egg on the right, **D.** Cape bulbul (*Pycnonotus capensis*) clutch with a Jacobin cuckoo (*Clamator jacobinus*) egg, **E.** Begging Common cuckoo chick, displaying the bright red gape, **F.** Differences in gape coloration between a Cape bulbul chick (top) and Jacobin cuckoo chick (bottom). Photos by Oliver Krüger (**A**, **D**, **F**), Nick Davies (**C**, **E**) and Bruce Lyon (**B**).

parasitism are not random events. With regard to nest height, the selection pressures from parasitism and predation are different (Fig. 10.7), but with regard to a nest architecture trait, cup depth, they are similar (Fig. 10.7). So nest site selection and nest architecture can influence reproductive success of

the host and there are instances of stabilizing and directional selection. The amount of overlap and difference between predation and parasitism and how they shape host reproductive success might help to gain a deeper understanding of host strategies towards brood parasitism (see Røskaft *et al.* 2002b for an example of the interaction between host behavior, habitat structure and parasitism risk).

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Applications of Reproductive Biology to Bird Conservation and Population Management

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11.1 INTRODUCTION

Population management encompasses a wide variety of activities, ranging from species conservation and recovery, to the control of pests and invasive species, to the sustainable harvest of wild populations. In all cases, however, the fundamental goal is to manipulate demographic processes so as to influence a population's trajectory to meet some specific objective. At its most basic, this means altering the number of juveniles that are recruited into the breeding population or changing the rate at which breeders are lost from the population. In this chapter we focus on the first of these processes and provide an overview of the ways in which an understanding of reproductive biology can be used to increase the number of recruits.

Although the specific goals of population management can be extremely different — e.g., to increase the production and survival of young in the conservation arena, or to decrease or eliminate them in the field of pest control — the underlying biological system available for manipulation is the same. In order to reproduce, birds must come into reproductive condition, find a suitable breeding area, select individuals with which to mate, produce large complex eggs that require substantial parental care, and, for most species, care for the young (Fig. 11.1). If birds can accomplish each of these steps successfully, there will be a pool of new individuals that become the next generation. Population management involves manipulating these stages to influence the direction of population change over time (Williams *et al.* 2001).

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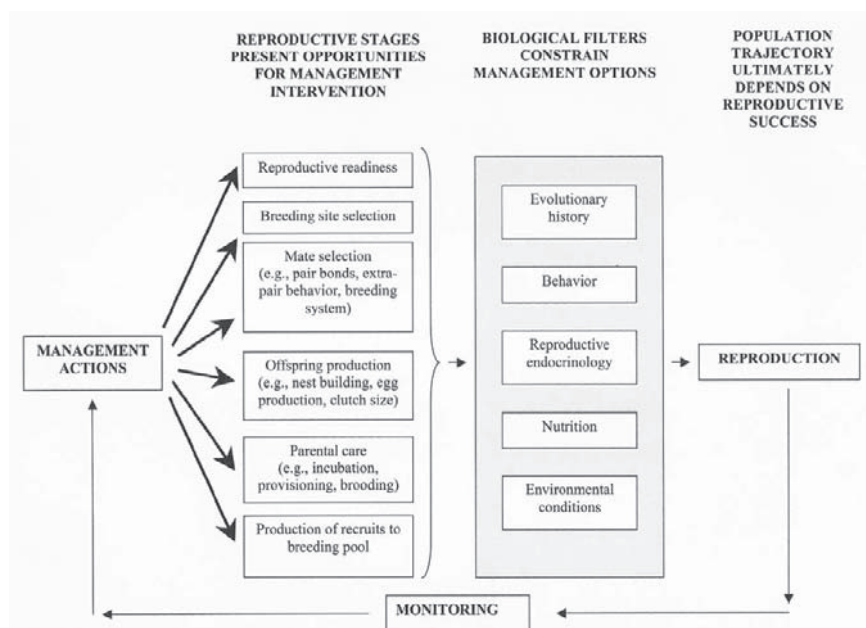


Fig. 11.1 Diagram of the relationships between the reproductive stages available for management manipulation and the biological constraints on management alternatives. In order to reproduce, birds must come into reproductive condition, find a suitable breeding area, select individuals with which to mate, produce large complex eggs that require substantial parental care, and, for most species, then take care of the young. Collectively, these processes determine the reproductive rate, which in turn influences population size and trajectory. This trajectory, and how management actions affect it, are tracked through monitoring.

Humans have been managing bird populations for millennia (Wood-Gush 1971; Sossinka 1982; Kear 1990). In combination with selective breeding, the development of husbandry techniques has allowed considerable increases in productivity of domesticated species (Korver and van Arendonk 1988; Gillespie 2004). These methods take advantage of knowledge about reproductive endocrinology, nutrition, genetics, and animal behavior to increase the rates at which eggs are produced and offspring mature. The production of more individuals in wild species has received parallel attention from managers who are intent on finding ways to increase the number of birds that can be harvested from a population for human use (Kear 1990; Kadlec and Smith 1992). In this context, the focus has been more on creating or enhancing habitat, to provide more opportunities for breeding and on reducing non-human sources of mortality (Payne 1992; Baldassarre and Bolen 1994), than on directly manipulating reproductive systems *per se*.

More recently, there has been a shift from a focus on food production and other direct benefits to humans to one that also emphasizes species conservation. One-eighth of the world's bird species are considered to be at risk of

extinction during the twenty-first century (BirdLife International 2004) and projections suggest that this number will continue to rise in the foreseeable future (Butchart *et al.* 2004). Habitat loss, fragmentation, and degradation are the primary causes of bird species endangerment, affecting at least 70% of threatened bird species (Wilcove *et al.* 1998; Owens and Bennett 2000; Li and Wilcove 2005). Overkill — caused by such things as over-harvest, depredation by exotic species, and disease — and habitat alteration by invasive species also affect large numbers of species (Collar *et al.* 1994; Wilcove *et al.* 1998; Owens and Bennett 2000; Gamarra *et al.* 2005; Keane *et al.* 2005; Li and Wilcove 2005). Climate change is expected to further exacerbate and complicate all of these issues by altering habitat distributions and changing the physiological constraints on where particular species can live (Walther *et al.* 2002; Parmesan and Yohe 2003; Root *et al.* 2003, 2005). Consequently, many more bird species may face extinction as a result of human impacts on global climate (Böhning-Gaese and Lemoine 2004; Thomas *et al.* 2004; Visser *et al.* 2004).

Causes of endangerment, and the effectiveness of techniques designed to recover populations, differ among species with different characteristics. For instance, species that are large bodied and have long generation times are more likely to be threatened by overkill, either through direct human persecution or the impact of introduced predators (Owens and Bennett 2000). These same species are also often slow to recover from population declines because of low reproductive rates and large-scale habitat needs. In contrast, species that have small body sizes and that are habitat specialists are more likely to be threatened by habitat loss (Owens and Bennett 2000) but may respond quickly to management. Some species also exhibit characteristic behaviors that increase extinction risk (Reed 1999). The links between the life history characteristics of species and endangerment create a direct connection between phylogeny and extinction risk. For example, families such as the Psittacidae (parrots) and Diomedidae (albatrosses) contain disproportionately high numbers of rare and endangered species (Beissinger and Snyder 1992; Bennett and Owens 1997; Butchart *et al.* 2004).

Simultaneous with this interest in enhancing the size or productivity of bird populations to meet societal goals, humans have also invested considerable energy in finding ways to reduce the population size of species considered to be pests. Again, the historical focus has been on species that directly impact humans, for example through crop depredation (Ward 1979; Decker and Avery 1990; Linz *et al.* 1996; Jones *et al.* 2000). Increasingly, though, population control is becoming an important issue in conservation biology too, for instance where introduced birds create problems for native species (Smith *et al.* 2005) or where native populations of one species have increased to the detriment of another (e.g., Wanless *et al.* 1996; Coates and Delehanty 2004).

Reproductive biology, clearly, is central to the processes that underlie population management, and has important roles to play both in identifying

management problems and finding solutions. Much of this book, then, relates at least indirectly to the issues discussed in this chapter, and other chapters provide detailed discussions of many areas of reproductive biology that could be used to manage bird populations better. Here, our goal is to illustrate the connections between this wealth of basic knowledge and specific management activities that are used to address applied questions. In such a small space, we can only begin to scratch the surface of this topic. Consequently, we provide only a brief summary of each step in the sequence of events that leads to successful breeding (Fig. 11.1), focusing on specific examples in which knowledge of reproductive biology has been used by managers. No doubt there are other connections that have, or could, be made, and it is our hope that this chapter will encourage further collaboration between biologists studying the details of reproductive biology and those that study population management.

11.2 REPRODUCTIVE READINESS

Avian reproduction is shaped by a mixture of evolutionary innovation related to the fundamental features that collectively characterize the order, and the constraints imposed by their reptilian (theropod) past (Prum 2002). With their high metabolic rate, birds have achieved extraordinary physiological capabilities, such as long-distance continuous flight, but are constrained by their high energetic needs (Blem 2000). Because normal maintenance activities are so costly, successful reproduction can occur only when birds can acquire sufficient energy, nutrients and minerals in excess of their high basic requirements. This situation is exacerbated because birds produce large, energy-rich eggs that require incubation and because their young have high metabolic needs of their own and must be fed frequently after hatching. The production of external eggs that need constant attention further constrains birds to breed only when there are adequate resources for them to remain resident in an area for long enough to raise their young. These conditions put additional limits on species that are migratory or that rely on ephemeral food supplies. Reproduction is constrained yet further to times when birds are not diverting excess energy and nutrients to other activities, such as feather molt (e.g., Moreno *et al.* 2001). Laysan albatross (*Phoebastria immutabilis*) and Black-footed albatross (*P. nigripes*), for example, replace only 20-90% of their wing flight feathers each year, and it has been suggested that molt patterns in large birds such as these might result from a tradeoff with reproductive constraints (Edwards and Rohwer 2005). This tradeoff, however, is apparently not present in some large species (e.g., White ibis *Eudocimus albus*, Heath *et al.* 2003). Given the many constraints they face, most wild birds breed seasonally in a manner timed to take advantage of abundant food resources.

While it is essential for a bird to be fertile during times of resource abundance, it is costly for birds to maintain functional reproductive tracts during times when breeding cannot succeed because of environmental (food,

weather, etc.) or other (molt, migration) constraints (Clark and Wilson 1981; Gill 1995). A fully developed reproductive tract also has a large mass (Lake 1981; Blackburn and Evans 1986; Proctor and Lynch 1993), which would add unnecessarily to the cost of flight during the nonbreeding season. Because of these costs, most wild birds severely diminish the size, mass, and functionality of the reproductive system during the nonbreeding season (regression) and regrow a functioning reproductive system at the onset of each breeding season (recrudescence). Temperate and high latitude birds have especially distinct breeding seasons, but cyclical reproduction is also characteristic of tropical and desert species, although in these environments some species cycle more than once each year or have a less sharply demarcated breeding season (Wingfield and Farner 1993; Johnson 2000).

From a management perspective, understanding the timing of regression and recrudescence is important because it determines when reproduction is possible and when certain reproductive behaviors are most likely to occur. In the wild, this timing is not something over which managers are likely to have control. Nonetheless, understanding when birds come into reproductive condition and when resources necessary for breeding are available, can be helpful in determining when and what management activities are most appropriate. For example, population monitoring might be most effective at times when birds are displaying and most obvious to human observers (e.g., Aspbury and Gibson 2004; Becker and Agreda 2005; see section 11.7). Such information is especially important for groups that have not been well studied, perhaps especially in tropical areas where reproductive activities are less well synchronized across species (Johnson 2000).

Undoubtedly, the single-most common management action used to help birds reach reproductive readiness is to provide and protect habitats that support prebreeding nutritional needs. For instance, the United States government purchases shallow ephemeral wetlands and manages them for seed-producing wetland vegetation and high invertebrate productivity in order to provide a good food supply for pre-breeding waterfowl. Maintaining a good diet at this time of year translates directly into improved body condition (Heitmeyer and Fredrickson 1990), which in turn is related to higher reproductive success (MacCluskie and Sedinger 2000).

Prebreeding nutrition has been especially well studied in waterfowl, but it is also gaining attention in other avian management systems. In western North America, for example, loss or alteration of the forb (i.e., non-woody, non-grass herbaceous plants) component of grass/shrubland ecosystems is thought to reduce female fecundity in some game birds. Female Greater sagegrouse (*Centrocercus urophasianus*), for example, shift from a diet high in sagebrush *Artemisia* spp. leaves to a diet high in forbs during the prelaying period of early spring, the only time of year in which sagebrush is not the major component of their diet (Barnett and Crawford 1994). Hence, adjusting agricultural grazing regimens to promote forb availability might provide a mechanism for increasing female fecundity in this species. Experiments on

captive Mountain quail (*Oreortyx pictus*) indicate that female fecundity can be manipulated directly by altering the nutritional value of the bird's food. In particular, the addition of certain plant nutrients to the diet of pre-breeding females leads to an earlier onset of gonadal recrudescence, a higher rate of egg-laying, and greater overall egg production (Delehanty 1997).

Not all nutritional intervention is intended to promote reproduction, and dietary manipulations have been proposed as a means of inducing temporary infertility in birds as an avian control method (Cook *et al.* 1996). The avian egg is characterized by a lipid- and nutrient-rich yolk that progressively "feeds" the embryo through the incubation period (Chapter 12). This process relies in part on the integrity of the semi-permeable vitelline membrane that surrounds the yolk. Permeability of this membrane depends on which lipids the female consumed during egg production, and consumption of particular lipids (e.g. conjugated linoleic acid) causes females to produce eggs that have overly permeable yolk membranes and are consequently not viable (Cook *et al.* 1996; Aydin and Cook 2004).

Another way of altering the conditions in which birds live, is to change the social environment. The importance of social facilitation (initiation or stimulation through conspecific interactions) to breeding is apparent in breeding site selection, with many species preferentially settling near conspecifics (Reed *et al.* 1999; see Section 11.3). Once a breeding site has been selected, social interactions also appear to facilitate mating and reproduction in many bird species, particularly in colonial species (Darling 1938; Orians 1966; Kress 1983). Hypothetically, then, the social environment of breeders might be manipulated to increase reproductive readiness or to facilitate reproductive output (discussed by Reed 2002, 2004). Manipulating cues to increase reproductive activities in small populations could stimulate reproductive behavior and ultimately increase population growth. For example, Pickering and Duverge (1992) stimulated pre-reproductive displays in a captive Lesser flamingo (*Phoenicopterus minor*) flock by putting up mirrors to give the appearance of more individuals. Artificial stimulation of this type also might be effective in wild settings, as shown by O'Connell-Rodwell *et al.* (2004) who combined visual and vocal displays (decoys, playback, artificial nests) to stimulate nesting behavior in a reintroduced population of Caribbean Greater flamingos (*P. ruber ruber*) that had not yet bred (Fig. 11.2A). Broadcasting the sounds of lekking birds (both vocalizations and other mechanically produced sounds) and placement of taxidermy mounts of adults are both regular features of prairie grouse restoration and are intended to provide social stimulation to grouse being released into potential breeding habitat (Coates and Delehanty (in press)).

In captivity, options for manipulating the reproductive system are more numerous than in the wild, and can range from directly altering the bird's physical and social environment to changing its physiological state. Manipulations in captivity could include something as simple as changing photoperiod (e.g., Smulders 2002) or supplementing diet. For example, the

breeding cycle of the King penguin (*Aptenodytes patagonicus*) can be shortened in captivity through supplemental feeding to increase chick growth (Jouventin and Mauget 1996). In other cases, more direct manipulation of the breeding cycle may be possible. For instance, although the use of endocrine therapy to bring captive individuals of rare species into breeding condition is in its infancy, Wingfield *et al.* (2000) have described how endocrine problems in captive settings could be investigated and possibly ameliorated in their study of Japanese crested ibis (*Nipponia nippon*), a critically endangered species in which many captive individuals had abnormal gonadotropin and sex steroid production. They point out that work on Japanese quail (*Coturnix japonica*) has shown that hormone therapy can correct problems with gonadal maturation, egg laying, and production of offspring, and these methods might be refined for use in other species. For now, however, approaches such as these are likely to be quite invasive and costly to implement, and realistically can be applied only to a relatively small number of individuals in situations where a species is in particularly dire straits.

The 1980s and 1990s saw substantial progress in understanding the reproductive endocrinology of birds which, in turn, has led to recent experimentation of endocrine manipulation to both promote and inhibit avian reproduction. This emerging field so far has focused largely on the control of pest species through the use of contraceptives, usually administered using food bait as a carrier (Dell'Omo and Palmery 2002; Johnston *et al.* 2003). For example, 20,25-diazacholesterol, a compound that appears to inhibit steroid formation by blocking the creation of cholesterol, itself a steroid precursor, may be an effective avian contraceptive (Johnston *et al.* 2003). An urban population of Rock pigeons (*Columba livia*) allowed to forage on corn bait treated with the endocrine disruptor Ornisteril, declined by 24% over a 3-year period (Dobeic 2003). The administration of nicarbazin, for which elevated levels in prelaying females results in egg infertility, is also being developed to control Canada goose (*Branta canadensis*) populations (Johnston *et al.* 2003). Most of the research in this field to date has been done on captive birds, such as Japanese quail (e.g., Yoder *et al.* 2004) or domestic Chicken (*Gallus domesticus*) (Johnston *et al.* 2002), but recent work has also addressed waterfowl species, such as Canada geese and Mallards (*Anas platyrhynchos*), that can be pests in urban settings (e.g., Yoder *et al.* 2005). The obvious concern with application of these methods to wild species, particularly when contraceptive chemicals are delivered through feed, is the potential harmful effects on non-target species.

11.3 BREEDING SITE SELECTION

The nature of a bird's breeding site is a primary determinant of the success or failure of its attempts to reproduce (Howard 1920; Lack 1966; Wiens 1976). The minimum function of breeding sites for all bird species is to provide a place to lay and hatch eggs. Even for the megapodes or "brush turkeys"

(Megapodiidae) of Australasia, the only avian group that does not provide post-hatching parental care, the “nests” are maintained by breeding males during the breeding season (Jones *et al.* 1995b). For most species, breeding sites are used for a variety of activities, such as attracting mates, providing foraging habitat, nesting, and raising young.

If one knows the habitat features that are used for breeding site selection, they can, in principle, be manipulated to alter population size. This is done most extensively for hunted waterfowl and other game birds, where habitat creation and restoration has been practiced for centuries with the goal of increasing species harvest (Payne 1992; Baldassarre and Bolen 1994). For example, altering water availability in arid and semi-arid environments is a common manipulation of the physical environment employed by wildlife managers to effect change in reproductive output. Despite their mobility, which facilitates seeking out water sources, desert birds can face substantial water stress due to the absence of locally available water (Dawson and Bartholomew 1968) and can be excluded from otherwise suitable habitat if sufficient water is not available. This effect is magnified by the relatively low mobility of chicks. In response, the placement of self-filling wildlife watering devices known as “guzzlers” has become a common management practice in arid regions (Delehanty *et al.* 2004). These devices are placed throughout potential breeding habitats to passively collect seasonal precipitation (usually winter rain or snow) into storage tanks that birds can access the following summer. Growing juvenile Mountain quail in western North America can exhibit remarkably high fidelity to these artificial water sources during periods of substantial water stress (Delehanty *et al.* 2004), suggesting that the benefits extend throughout the reproductive cycle.

Habitat creation and restoration also have become central tools in the conservation of endangered species and are particularly important because habitat loss and degradation affect the majority of the world’s threatened bird species (Owens and Bennett 2000). Habitat manipulation clearly can take many forms, but might be as simple as providing artificial ledges or platforms for nesting (e.g., Northern bald ibis *Geronticus eremita*, Hirsch 1977, Osprey *Pandion haliaetus*, van Daele and van Daele 1982, respectively). A frequent approach is to provide nest boxes, which has helped to increase the number of available nest sites in a wide variety of cavity-nesting species, ranging from waterfowl (Kadlec and Smith 1992; Bellrose and Holm 1994) (Fig. 11.2B), to raptors (Korpimaeki 1985; Wheeler 1992), to passerines (Willner *et al.* 1983; Minot and Perrins 1986). Similarly, the creation of nest cavities in trees has become an important tool in the recovery of Red-cockaded woodpecker (*Picoides borealis*) populations in the southeastern United States. This endangered species is unusual because it lives in fire-maintained pine savannah, where it makes cavities only in live trees and is limited by the availability of mature pines (*Pinus* spp.) (Jackson 1994). Copeyon and her colleagues solved the technical problem of drilling nest cavities in live trees without causing them to fill with sap, and showed that birds rapidly

occupied newly created nest sites (Copeyon 1990; Copeyon *et al.* 1991). More recently, simpler methods using artificial cavities for this species have come into use (Saenz *et al.* 2001). Identifying and refining artificial breeding site features to better attract and house target species can be an important area of conservation research (e.g., Lalas *et al.* 1999; Stamp *et al.* 2002).

Within a suite of suitable habitat patches, it is sometimes also possible to manipulate where birds settle. This might be done because of a desire to attract individuals to newly restored sites (Ward and Schlossberg 2004), to sites that are protected (Podolsky 1990; Kress 1997), or to draw birds away from so-called ecological traps where reproduction is low or mortality is high (Kokko and Sutherland 2001). Not only can nest site features be manipulated, but one also can alter other cues used during breeding site selection (Reed 2004). In particular, conspecifics frequently provide cues to the suitability of habitat, and affect settlement decisions by prospective breeders (Stamps 1988, 1991; reviewed by Reed *et al.* 1999). Decoys fashioned to resemble the target species or sound recordings of colonies have been used to induce colonial seabirds to establish new breeding colonies (e.g., Kress 1978, 1983, 1997; Kress and Nettleship 1988) and to attract wading birds to foraging sites (Crozier and Gawlik 2003). Potential cues of breeding site quality using decoys have been further refined in the Laysan albatross, where decoys of chicks and of adults in courtship poses were displayed (Podolsky 1990). Similarly, Sarrazin *et al.* (1996) used white paint to simulate the appearance of feces on cliff faces at sites once used for conspecific breeding in order to attract Eurasian griffons (*Gyps fulvus*).

Birds might also respond to cues from other species through heterospecific attraction. For instance, some beach-nesting shorebirds frequently nest in association with colonial seabirds (e.g., Burger 1987; Alleng and Whyte-Alleng 1993; Warnock *et al.* 2002). Such behaviors are coming under greater scrutiny in a wider variety of bird species (e.g., Mönkkönen and Forsman 2002) and eventually could lead to more sophisticated tools for manipulating the behavior of species in ways that provide management benefits.

Breeding site selection might also be manipulated to draw species that are perceived to be a nuisance away from areas where they are causing problems. For instance, Caspian terns (*Sterna caspia*) became a problem to salmon (*Oncorhynchus* spp.) restoration efforts along the Columbia River in the western U.S.A. following a major shift in nest site selection, and rapid population increase, associated with the creation of sand islands from deposited dredge material (Roby *et al.* 1998; Suryan *et al.* 2004). Collis *et al.* (2001, 2002) found that juvenile salmon migrating from their hatching grounds to the ocean made up over 70% of the terns' diet in parts of the river. Using bioenergetic models, they estimated that a colony of over 9,000 pairs took over 8 million and 12 million salmon in two years, respectively, representing approximately 15% of the juvenile salmonid population reaching that part of the river (Roby *et al.* 2003). Caspian terns were successfully relocated to a site where they would have less impact on salmon populations

by creating nesting habitat at the new site, using social attraction techniques (decoys and sound playback), and predator control, while simultaneously discouraging terns from nesting at the old sites by planting vegetation and erecting fencing, wiring, and streamers (Roby *et al.* 2002). The colony completely shifted breeding sites within three years, and the proportion of the birds' diet made up of salmon dropped to less than half compared to its previous breeding site.

There are, of course, limits to the degree to which a species' breeding site selection can be manipulated. A species' evolutionary history, for instance, often constrains nest site selection, even when certain choices seem maladaptive in the context of modern human activities. Certain taxonomic groups, for example the Anseriformes, Galliformes, and Charadriiformes, are dominated by species that nest directly on the ground, and, at least among passerines, ground-nesting species suffer greater depredation than do species that nest in trees (Terborgh 1989). Many species, even habitat generalists, are relatively inflexible in the types of nest sites they will use. Exceptions occur, but they are usually not species that are a focus of management attention, simply because generalists typically are not a focus of conservation concern. One class of exceptions includes rare species that are able to occupy novel habitats that inadvertently mimic their natural habitat. Peregrine falcons (*Falco peregrinus*) for instance typically nest on cliff faces, but in parts of their range where this habitat does not occur, they sometimes nest on power line towers or high-rise buildings (White *et al.* 2002). In other cases, it might be possible to encourage greater use of rarely occupied nest sites. Common moorhens (*Gallinula chloropus*), for example, usually nest in dense emergent marsh vegetation but individuals occasionally nest in trees or in artificial nest boxes (Bannor and Kiviat 2004). Recognizing this potential flexibility, elevated, enclosed nest sites are now being used in an attempt to protect nests from terrestrial predators in the endangered Hawaiian moorhen (*G. c. sandvicensis*; Reed *et al.* personal observation).

Breeding site creation is not always a simple matter of recreating a breeding structure and placing it in a suitable habitat and the technique should be used with care. For example, Wood ducks (*Aix sponsa*) are obligate cavity nesters, and there is a long history of providing nest boxes as a management tool (Fig. 11.2B; Bellrose and Holm 1994). Wood ducks also are conspecific brood parasites, however, and high parasitism rates can cause abnormally large clutches that cannot be effectively incubated and in which eggs frequently get damaged. At high population densities, reproductive success can be reduced sufficiently to cause populations to crash (Haramis and Thompson 1985; Eadie *et al.* 1998). Semel *et al.* (1988) and Semel and Sherman (1995) found that the location of Wood duck boxes affects the rate of brood parasitism, with higher parasitism rates when boxes are placed in the open and at high densities. These results suggest that hiding nest boxes, and spacing them widely, can reduce parasitism rates and thus increase the effectiveness of the management.

11.4 MATE SELECTION

Mate quality, and the number of individuals with which a bird is able to reproduce, are important determinants of fitness, and birds exhibit sophisticated mate selection behaviors (see Chapters 1-7). Cues used to assess mate quality differ among species but often are associated with body size, body condition (e.g., stored fat), singing rate, or traits displayed in the plumage or skin (e.g., Olson and Owens 1998; Hill 2002; Chapters 1,2,3,5,6). Displayed traits can either provide direct or indirect information about individual quality. In some species, plumage cues can be obvious, such as the large, elaborate tails of Indian peafowl (*Pavo cristatus*) and other species (Darwin 1871; Loyau *et al.* 2005). Recent research, however, has also shown that some important cues have been overlooked; for example, because they are visible only in the ultraviolet spectrum, which is not directly perceived by humans (e.g., Andersson *et al.* 1998; Hunt *et al.* 1999; see also Chapter 1).

Although mate selection is largely studied in the context of its effects on individual fitness, an understanding of the decisions made when a bird chooses which individuals it will copulate with can potentially provide opportunities to manipulate mating patterns in order to achieve some management goal (Reed 2002). For example, mate availability in some rare species could be increased either (a) by translocating individuals (e.g., Kakapo *Strigops habroptilus*, Triggs *et al.* 1989; Po'ouli *Melamprosops phaeosoma*, Groombridge *et al.* 2004, although the attempt for this species failed), (b) by attracting individuals to a new site via decoys or playback (see sections 11.2 and 11.3), or (c) by increasing the amount of a limiting resource (see Red-cockaded woodpecker example in section 11.3). Within very small populations, where there can be concern about inbreeding depression, one theoretically could decrease the loss of genetic variability by altering mate selection patterns (Blumstein 1998; Reed 2002). For instance, one could limit the number of matings between close relatives or decrease the variance among individuals in the number of young they produce (Crow and Kimura 1970). To achieve these results, one would have to physically interfere with mating decisions, by limiting which individuals are able to breed together or by changing the apparent quality of some individuals in order to alter copulation patterns. In captive populations, genealogies can be generated from studbook records in order to determine which individuals should be allowed to mate with each other to achieve genetic conservation. For example, one important aspect of the Guam rail (*Gallirallus owstoni*) captive breeding program was to minimize the loss of genetic variability from the small captive population, prior to reintroduction of the species to the wild. This was done by determining kin structure using molecular markers and analyzing alternative pairing scenarios (Haig *et al.* 1994; Haig and Ballou 1995). In the wild, genealogical information is less likely to be available (though see Blackwell *et al.* 1995), and directing mating patterns is much more difficult to achieve than in captivity. Ecologists, however, have influenced mate selection in many

experiments designed to test basic questions about animal behavior by altering the appearance of individuals (Andersson 1982; Burley 1986; Witte and Curio 1999; Safran *et al.* 2005), and this approach could theoretically be used in extreme situations where a species' persistence was in jeopardy.

If mate selection is based on territory quality or external cues related to individual quality, this further opens the possibility of manipulating mate selection. For example, bower birds have specialized structures designed to attract mates, and some structures are adorned with bright objects (Diamond 1986). Borgia (1985) found that removing most of the decorations at the bowers of Satin bowerbirds (*Ptilonorhynchus violaceus*) reduced mating success. Some such manipulations, however, might result in increased intra-sexual competition with no concomitant increase in mating success, as Madden (2002) found when he manipulated display items of Spotted bowerbirds (*Chlamydera maculata*).

It has been predicted that species with polygynous mating patterns would be less vulnerable to extinction than are species with monogamous mating systems, particularly when population sizes are small (Legendre *et al.* 1999; Møller and Legendre 2001). This is due in part to Allee effects that cause population growth rates to decline as populations get smaller. Random variation can cause small populations to have skewed sex ratios, and a shortage of males in a polygynous system is predicted to be less likely to limit reproduction by females (Courchamp *et al.* 1999). Species that are socially monogamous, however, do not appear to be at more risk of extinction than are polygamous species (Morrow and Pitcher 2003), nor are they less likely to become established following introduction or translocation (Bessa-Gomes *et al.* 2003; see also McLain *et al.* 1995, 1999). Moreover, females in some socially monogamous species apparently overcome a shortage of males by engaging in extra-pair matings (Conover and Hunt 1984). Recent modeling studies show that the relationship between mating system and extinction risk are not systematic and instead depend on local population size, operational sex ratio, and the details of density-dependent feedback on vital rates (Bessa-Gomes *et al.* 2004; Sæther *et al.* 2004). Consequently, mating system *per se* does not appear to identify particularly extinction prone or resilient species.

11.5 PRODUCTION OF OFFSPRING

Once a breeding site and mate have been selected, birds must build nests and produce eggs. Knowledge about reproductive biology can be valuable to managers both because it can help to identify situations where the natural reproductive capacity of a population is compromised and because it can provide insights into the ways in which the rate of offspring production can be altered to meet management goals. Understanding the phylogenetic constraints that species face is also important because they might influence the range of options available to managers. For instance, if clutch size is fixed certain management techniques may not be plausible.

Various studies of environmental contaminants illustrate the way in which an understanding of reproductive biology can help to better address a management problem. Well known research on the declines of predatory birds lead to the discovery that pesticides such as dichlorodiphenyltrichloroethane (DDT) can alter the structure of eggshells, making them more vulnerable to premature cracking and resulting in reduced production of young (Hickey and Anderson 1968; Ratcliffe 1970). Similarly, more recent work has shown that nest building behavior in Tree swallows (*Tachycineta bicolor*) differs between area with high levels of polychlorinated biphenyl (PCB) contaminants and control areas. These differences result in lower quality nests that are less likely to fledge young in the contaminated area (McCarty and Secord 1999).

Once sources of nest failure have been identified, methods for removing the problem can be developed. In the case of environmental contaminants, this can be done through legislative means or through environmental clean-up activities. In other situations more direct management might provide a means by which the production of young can be increased. For instance, several endangered species in North America are thought to have benefited from the control of Brown-headed cowbird (*Molothrus ater*) populations (Eckrich *et al.* 1999; Whitfield *et al.* 1999). Sometimes, however, management activities designed to enhance productivity prove not to be as successful as they are perhaps assumed to be, as indicated by a meta-analysis of studies that have investigated the impact of predator control on bird populations (Côté and Sutherland 1997).

Increasing reproductive success at this stage of reproduction, however, is often costly and can require the use of quite invasive methods. Logistical challenges and idiosyncratic differences among species often also require extensive trial-and-error to develop effective methods. Consequently, this general approach to management is used in relatively few species and is usually considered a last resort in the conservation of rare species. In cases where alternative management strategies have failed or are not available, however, a common method of increasing the offspring production rate is to remove eggs from nesting birds and take them into captivity where they can either be incubated artificially or by a foster parent of another species (e.g., Fyfe *et al.* 1977). This general approach has three variants. First, eggs can be removed from the nest of a species that normally cannot rear all of the young that normally hatch. Second, eggs can be removed sequentially from a partially complete clutch, so that the female lays more eggs than normal in order to obtain a complete clutch. Finally, entire clutches are sometimes removed to induce the bird to lay a replacement clutch. An example of this approach comes from the Mauritius kestrel (*Falco punctatus*) population recovery program (Jones *et al.* 1995a). Here, researchers (a) removed eggs as they were laid to increase total egg production, and (b) removed entire clutches of eggs, causing females to lay replacement clutches (referred to as double-clutching). Researchers found that the second approach was more effective at

increasing egg production in this species. In principle, removed eggs or clutches can be transferred among nests in both wild and captive settings. Before employing this method, however, it is critical to understand the biology of the target species sufficiently well to ensure that additional eggs will be laid, and that the management activities will not simply result in nest abandonment. Clutch size reduction, for instance, can lead to nest abandonment in some species (e.g., Wilson's phalarope *Phalaropus tricolor*, Delehanty and Oring 1993), and the likelihood of abandonment can be affected by the severity of the clutch reduction (e.g., Mallard, Ackerman and Eadie 2003). Consequently, it is important to know when best to remove eggs in order to ensure that relaying occurs and that abandonment does not happen.

Another labor-intensive approach to increasing reproductive output that could be used in captive-breeding settings is artificial insemination. Although artificial insemination has been used mostly in domestic species (Perry 1968), there are notable uses in non-domestic bird species such as falcons (Gee 1995), semi-domestic species such as Emus (*Dromaius novaehollandiae*) (Malecki and Martin 2004), and captive wild birds (Jones and Nicolich 2001). Semen has been gathered from birds via natural copulation with dummies or some other receptacle (Berry 1972; Boyd 1978) and by massaging the cloacal protuberance (or phallus, in species that have one) of a captured male (Gee 1983); electroejaculation techniques conducted under anesthesia are available, but are not commonly used for wild species (Gee 1995). Females subsequently are inseminated with a device that, preferably, achieves deep vaginal (rather than cloacal) semen placement (Gee 1995). Artificial insemination has been used successfully for some wild bird species, such as Golden eagle (*Aquila chrysaetos*), Peregrine falcon (Blanco *et al.* 2002), and Aleutian Cackling goose (*Branta hutchinsii leucopareia*; Gee and Sexton 1990). Collecting viable sperm, storage, and insemination can cause problems, however and methods need to be developed for each species (e.g., Penfold *et al.* 2001). Because the methods are time intensive, sperm collection and insemination can result in injury, and sperm storage is temporary (e.g., Saint Jalme *et al.* 2003), artificial insemination should be viewed as a last resort in species' conservation efforts, and would most often be done as part of a captive breeding program (Hutchins *et al.* 1995, Saint Jalme 2002).

Theoretically cloning also could be used to create new embryos for rare species, and therefore increase reproductive output (Lanza *et al.* 2000; DeSalle and Amato 2004). Cloning methods, however, are in the early stages of development and birds have not been a primary research focus. Although cloning might attract public attention because of its "science fiction" quality, we do not foresee a future where cloning plays a significant role in species conservation, except as a last resort for highly endangered species. Even in these cases, it is likely to be difficult to create populations with sufficient genetic variability to be viable over the long term (e.g., Loi *et al.* 2001; Ryder 2002; Gómez *et al.* 2004). Although the preservation of genetic material

suitable for future cloning efforts may be a worthwhile activity, in the near term it is probably more important to direct resources towards preventing species from becoming highly endangered in the first place (DeSalle and Amato 2004).

Manipulations designed to increase reproductive output are effective only within the context of (or are limited by) species-specific behaviors. For example, cross-fostering and double-clutching using surrogates could exacerbate inbreeding in small populations if inbreeding avoidance is learned via early familiarity. That is, if inbreeding avoidance is a consequence of not mating with brood mates, then splitting clutches for rearing could prevent sibling recognition. Conversely, if unrelated individuals are raised together they might be unwilling to mate once they are adults. Early learning also can affect species recognition in ways that influence the selection of appropriate mates once maturity is reached (Reed 2004). An example of this arose when Whooping cranes (*Grus americana*) that came from eggs that were cross-fostered into a Sandhill crane (*G. canadensis*) nest courted members of their foster species, rather than their own (Mahan and Simmers 1992).

Complex technological or manipulative solutions to the problem of increasing the production of young in captive settings may not, however, always be necessary. For instance, a study of captive Humboldt penguins (*Spheniscus humboldti*) that correlated husbandry conditions with measures of reproductive success using data from many different zoo collections, produced a number of simple recommendations for improving the reproductive success in captive populations that could be implemented simply by changing the conditions in which birds were kept (Blay and Côté 2001).

The converse of the problem of enhancing reproduction for species of concern is to reduce reproductive success of birds considered to be pest species. The most common approach has been to destroy eggs, through procedures such as oiling or puncturing (e.g., Lewis and Malecki 1984; Blackwell *et al.* 2000). These methods are preferred to egg removal or crushing because they prevent obvious clutch loss, which increases the chance that the parents will continue to incubate the dead eggs rather than produce a new clutch. An alternative is to prevent egg laying through the use of chemical contraception (e.g., Hurley and Johnston 2002; Dobeic 2003; Johnston *et al.* 2003; section 11.2). This approach has not been used extensively for any type of wildlife but its limited use on White-tailed deer (*Odocoileus virginianus*; Rutberg *et al.* 2004) and other mammals suggests to us that it is not likely to be a promising avenue for the control of most avian pests (see also Barlow 2000).

11.6 PARENTAL CARE

For the production of young to influence population dynamics, it must result in the recruitment of birds to the breeding population. In almost all birds, this requires some level of post-hatching care. The type and extent of care,

however, varies greatly among species and understanding the requirements of a particular species can provide important management insights. For species with altricial young that are completely helpless, parents must provide all basic maintenance activities, such as providing their young with food and protecting them from the elements and predators. For species with precocial young that can get around on their own and find their own food, parents still provide considerable protection by brooding, by warning against and distracting predators, and by guiding the young to safe areas. In some species, parental care also involves the transmission of complex behavioral information. For example, geese and other species usually migrate in family groups, suggesting that young learn migration routes from their parents.

Understanding both the amount and type of parental care needed by a species is especially important when breeding endangered species in captivity, both for biological and logistical reasons (Hutchins *et al.* 1995). When rare species are bred in captivity, surrogate parents are often used to raise the young. This method leaves the actual parents free to produce additional clutches (see section 11.5). For this approach to work, however, it is critical that the foster chicks be raised appropriately.

Foster parents are sometimes birds of another, usually closely related, species. For instance, Madagascar turtle-doves (*Streptopelia picturata*) have been used to raise endangered Pink pigeons (*Columba mayeri*) from Mauritius (McKelvey 1976; Bruning 1989). For some species, however, the use of foster parents from another species can cause unanticipated problems (see section 11.5), and for others there might not be appropriate surrogate parents available. This could be a particular problem where extensive cultural learning is important. Consequently, humans sometimes take on the parental role. This situation also raises concerns that young birds might learn inappropriate behaviors from the humans that raise them and that they might fail to learn key behaviors that are important for survival in the wild. Hand-reared individuals, for example, are often tamer and less aware of potential threats than are their wild counterparts, and this can result in high mortality when they are released into the wild (Hutchins *et al.* 1995). Studies of captive parrots, for example, have shown that hand-reared birds have lower reproductive success than individuals raised by their parents (Myers *et al.* 1988) and that hand-reared birds do not survive well when introduced into the wild (Wiley *et al.* 1992).

If captive breeding is to be attempted, understanding the mechanism by which imprinting occurs can be extremely helpful in designing effective husbandry techniques. For instance, initial attempts to hand rear Andean condors (*Vultur gryphus*) resulted in the offspring imprinting on their human keepers, but this problem was alleviated by minimizing contact between birds and humans and the use of condor-like hand puppets to feed the chicks (Bruning 1983). Understanding the timing of imprinting also can be helpful, as it allows one to identify periods when extreme measures are most critical (Hutchins *et al.* 1995).

Appropriate predator recognition and response behaviors are also learned by some species from their parents, and therefore birds reared in captivity sometimes must be taught the appropriate cues and responses. For example, passive and active models of predators have been used to investigate the responses of endangered species, such as the Takahe (*Porphyrio mantelli*; Bunin and Jamieson 1996) and New Zealand robin (*Petroica australis*; McLean *et al.* 1999), to predators, and can be used to train them to recognize predators and respond appropriately (I. Jamieson, personal communication). Takahe, for example, were tested by exposing them to a stuffed Stoat (*Mustela erminea*), which was placed on a box that covered a small remote control car, such that the box hid the wheels (Fig. 11.2C). The Stoat could then 'emerge' from the cover of a larger box hidden in vegetation, as desired by a human observing from some distance away. In initial tests, a young Takahe that had been raised by foster-parents of a species with a well developed defensive response to Stoats exhibited more appropriate anti-predator behaviors than did a control Takahe that had been raised by its true parents (Bunin and Jamieson 1996).

Captive breeding has created both problems and opportunities for managers. Conservation efforts for Whooping cranes, for example, have emphasized captive breeding as a mechanism for increasing population size. In order to successfully introduce the captive-bred cranes into the wild population, however, it is necessary to teach them where they should migrate. Because these birds do not have wild parents who can teach them, managers have developed innovative training methods, which have involved imprinting the youngsters so that they follow ultralight aircraft and then using the aircraft to lead them to wintering grounds (Fig. 11.2D). This approach also has been used in Sweden to reintroduce Bean goose (*Anser fabalis*) and Lesser white-fronted goose (*A. erythropus*) populations (Morner 1986). Although the use of ultralight aircraft, and other motorized vehicles, was developed to solve a problem caused by the complexity of a species' biology, the solution has created new opportunities for conserving species. The use of motorized vehicles to teach migration routes to young birds, for example, now makes it possible to manipulate migratory pathways and create populations in new places (Ellis *et al.* 2003).

Overall, however, captive breeding is a logistically difficult and typically expensive endeavor (Snyder *et al.* 1996). Understanding the biological requirements of parental care, therefore, can help managers not only to ensure that it is done well but also to decide whether it should be attempted in the first place. Because species differ in the amount and type of parental care they need, they also differ in their suitability for captive breeding. Altricial young that need to be fed frequently, for instance, generally require far more work than do precocial young that can feed themselves. Consequently, species with precocial young may be logistically easier to raise in captivity than species with altricial young, and it is not surprising that most domesticated species are highly precocial (although this relationship is confounded by the fact that domesticated species also tend to be relatively large, which makes them more

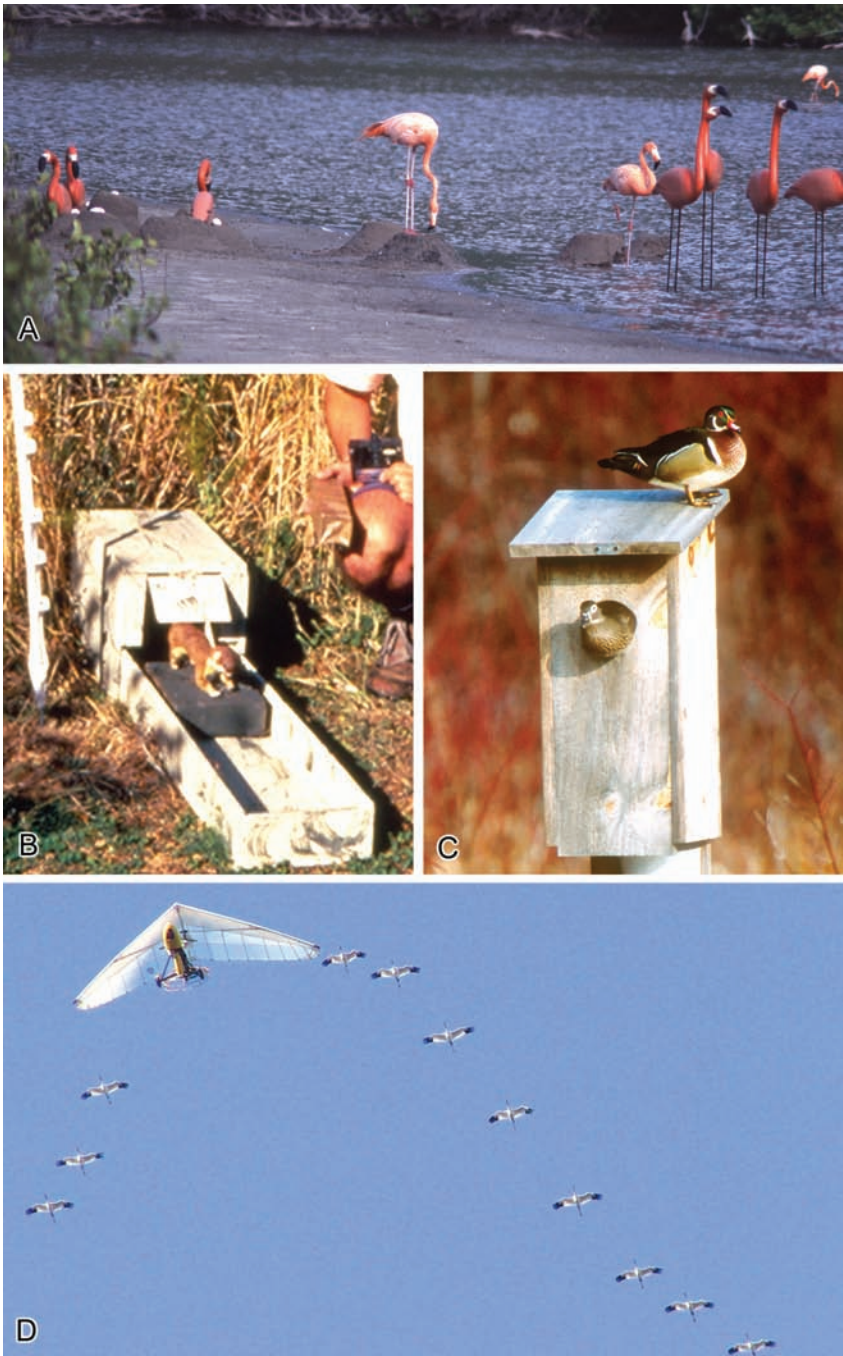


Fig. 11.2 A. Wooden flamingos and eggs (in artificial mud nests) alongside living Caribbean Greater flamingos (*Phoeniconais ruber ruber*). B. Male (top) and female

Fig. 11.2 Contd. ...

suitable for meat production). On the other hand, many species with precocial young are also large and take a relatively long time to reach maturity, meaning that parental care might require a longer-term investment than for smaller species with altricial young (e.g., compare cranes to passerines). Similarly, some species with altricial young are easier to raise than others. For instance, species that are insectivorous and need feeding multiple times an hour require a much greater time investment than do altricial carnivores, which can be fed less frequently and more easily.

Despite the extensive opportunities to manipulate parental behavior in captivity, there probably are limited options to make equivalent manipulations in wild populations. Opportunities to directly manipulate incubation and brooding behaviors, or predator defense, seem unlikely. Food provisioning, however, could indirectly influence all of these things by decreasing the amount of time parents need to be away from a nest, decreasing the amount of time a chick or fledgling is exposed to predators, and improving body condition for both adults and young (e.g., Dewey and Kennedy 2001). Some food provisioning experiments, however, have found that supplemental feeding of chicks had no effect on offspring condition or fledging success (e.g., Leach's storm-petrel *Oceanodroma leucorhoa*, Takahashi *et al.* 1999; House wren *Troglodytes aedon*, Styrsky *et al.* 2000), again pointing to the need to understand the idiosyncratic differences that arise in different situations. Food provisioning might benefit chicks and adults in other ways as well. There is evidence from captive-bred birds that increased activity and energy expenditure during reproduction can decrease antibody responsiveness (Deerenberg *et al.* 1997), which suggests that there could be health benefits if reproductive effort were reduced, e.g., through supplemental feeding. Supplemental feeding also has been associated with reduced chronic stress (as measured by baseline and stress-induced corticosterone levels) in male Song sparrows (*Melospiza melodia*) with chicks (Clinchy *et al.* 2004); chronic stress can lead to decreased reproduction and death in some circumstances (Wingfield *et al.* 1997).

In wild populations, pollutants can interfere with parental care, and therefore measuring parental behavior might function as a biological indicator of some environmental contaminants (Døving 1991; Cohn and MacPhail 1996; Kulig *et al.* 1996; Reed 2004). Grue *et al.* (1982), for example, found that European starlings (*Sturnus vulgaris*) exposed to an organophosphate insecticide (dicrotophos) exhibited reduced attentiveness to their offspring.

Fig. 11.2 Contd. ...

(emerging) Wood ducks (*Aix sponsa*) using an artificial nest box. **C.** Stuffed Stoat (*Mustela erminea*) used to investigate the response of captive-bred Takahes (*Porphyrio mantelli*) to predators. **D.** Whooping cranes (*Grus americana*) following an ultralight airplane to learn a new migration route. Photographs courtesy of: A, Timothy Rodwell, Stanford University; B, © Paul Fusco, Connecticut Department of Environmental Protection; C, Ian Jamieson, University of Otago; D, © Operation Migration.

A single oral dose of the pesticide resulted in females making fewer trips to feed their young and increased the amount of time that the mothers spent away from their nests. As a result, nestlings lost weight. European starlings also reduced food provisioning to chicks when exposed to PCBs, resulting in decreased chick survival (Arenal *et al.* 2004). Interference of parental behavior due to chemical exposure, with subsequent effects on chick survival, has been documented for other species as well, including Ringed turtle-doves (*Streptopelia risoria*; Peakall and Peakall 1973), Tree swallows (Bishop *et al.* 2000), and Common loons (*Gavia immer*; Nocera and Taylor 1998). Using these behaviors as bioindicators would require an adequate database of "normal" behaviors against which to compare observed behaviors, which may limit the utility of the approach (Kulig *et al.* 1996; Peakall 1996). In cases where there is a high risk of contamination, however, aberrant parental behaviors might provide an inexpensive means of determining whether more detailed study is warranted.

11.7 MONITORING

Throughout this chapter we have focused on ways in which reproductive biology can be used to manipulate population sizes. A separate, extremely important, component of population management involves monitoring population size in order to assess when management is necessary and whether management actions are successful. Because much monitoring occurs during the breeding season, many methods require a basic understanding of reproductive biology in order to maximize their effectiveness. For instance, many survey protocols are designed to count the number of singing birds, which requires an understanding of when singing activity is likely to peak, both seasonally and during the daily cycle (Ralph and Scott 1981; Bibby *et al.* 1992). Other surveys are designed to monitor the number of nests or young produced, and thus must be designed with a knowledge of the basic breeding biology of the target species in mind.

In some cases, understanding breeding behavior might be especially useful in designing an appropriate monitoring program. For example, species are often easiest to count when they are aggregated into a small area, and so identifying situations where birds gather in groups as part of their reproductive activities can be useful. This approach is particularly helpful when the locations where aggregations occur are predictable from year to year. Monitoring colonial species, such as seabirds and herons, consequently often occurs at nesting colonies (e.g., Dyer *et al.* 2005), and lekking species, such as bustards and various grouse, are often monitored at traditional display sites (e.g., Lane and Alonso 2001).

Situations also arise where an understanding of a species' reproductive behavior can be useful in designing methods that improve upon passive counting. For instance, some species are difficult to survey because they are cryptic, live in dense vegetation, or are largely nocturnal. Such species often communicate largely through sound and their presence and abundance can

be effectively determined using playback surveys in which vocalizations are broadcast and the responses counted (e.g., Conway and Gibbs 2005). For any of these methods to be useful, however, they must be based on a detailed understanding of the reproductive biology of the target species. For instance, singing rates in some species decline after a male has found a mate (Gibbs and Wenny 1993; Tyler and Green 1996), meaning that high levels of singing in an area could indicate the presence of high numbers of unpaired males — which, in an apparent paradox, could be a sign of poor habitat conditions (McGregor *et al.* 2000).

11.8 CONCLUSIONS

We have organized this chapter around the biological processes that collectively constitute reproduction (Fig. 11.1), rather than around the work that occurs in particular sub-disciplines or on specific conceptual ideas. The reason for this organization is to emphasize that effective management requires that one intervene with the breeding cycle wherever an intervention is most likely to achieve a desired goal. Recognizing where interventions will be most useful in order to meet a specific goal, therefore, requires both a broad base of information about all aspects of a species' biology as well as detailed knowledge of the precise mechanisms involved in different areas of reproductive biology. Consequently, there are many potential ways in which specialists collaborating with applied ecologists can contribute to the discovery of novel solutions to management questions.

The ultimate goal of most population management is to effect change in a population's size. In many cases, perhaps most, this is done indirectly by manipulating the breeding habitat in which a species occurs. Directly manipulating the reproductive biology of individuals is generally more of a logistical challenge, simply because it becomes difficult to apply specific treatments to large numbers of birds. This reason is probably why approaches, such as the development of contraceptive methods for species that are considered pests, have not been successfully applied at large scales in wild populations. Many aspects of reproductive biology, therefore, may be most relevant in conservation settings where populations are already small and the number of birds involved is logistically manageable. Many potential interventions, however, are also very intrusive and can be expensive to implement. Consequently, the possible benefits of activities such as cross-fostering and captive breeding should be weighed against the risks of interfering with populations that are already in a precarious situation and against the benefits that can be gained by directing money towards other activities such as habitat improvement.

Overall, though, there are clearly a wide range of opportunities to apply basic research on the reproductive biology of birds to the general problem of altering rates at which young birds are recruited into a population. When set in the context of other demographic processes, this information can be used to address many diverse questions in applied avian ecology.

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Embryogenesis and Development

Bodo Christ and Martin Scaal

12.1 INTRODUCTION

The avian embryo has a long history as a subject of embryological observations. This is not surprising since the egg is universally available and the embryo is readily accessible because it is a self-supplying system and does not depend on the mother for its nutrition. The first description of avian embryology goes back to antiquity. It was Aristotle (384-322 B.C.) who gave a detailed description of the chick embryo in his *Historia animalium*. He observed the beating heart of the embryo and called it "*Punctum saliens*" (jumping dot). In the Renaissance period, embryological studies were taken up again by Italian naturalists and anatomists. Ulrisse Aldrovandi (1522-1605) described the early stages of chick development in his *Opera Omnia*. Further observations were published by Fabricius ab Aquapendente (1537-1615) in his "*De Formatione Ovo et Pulli*". Harvey (1651) published observations on the developing chick embryo in his "*Exercitatione de generatione animalium*". He was the first who stated "*omne vivum ex ovo*". Malpighi (1628-1694) an Italian anatomist, laid the foundation for the modern understanding of avian embryology through his published works: "*De Formatione Pulli in Ovo*" and "*De Ovo Incubato*". This promising beginning of avian embryology was continued by Haller (1708-1777), who was an anatomist at the University of Göttingen and a famous poet. His findings were published in "*Sur la formation du coeur dans le poulet*" and "*Elementa Physiologiae Corporis Humani*". Very detailed descriptions of chick development were published by von Baer (1828), Remak (1850), His (1868), Duval (1889), and Lillie (1908).

In the twentieth century, the avian embryo became the subject of microsurgical approaches such as extirpations, isolations, and transplantations of anlagen to study tissue interactions. In the seventies of the last

century cell lineage studies could be performed by means of quail-chick chimerization which was introduced by Le Douarin (1969). To modern embryologists, the avian embryo offers an accessible system that allows the combination of microsurgical approaches with molecular studies. Transplantation experiments and application of signaling molecules can be combined with *in situ* hybridization and Northern analysis. It is now possible to over-express a gene or to inhibit its expression by retroviral transfection and electroporation of sense and RNAi constructs, and to analyze the effect after certain reincubation periods.

12.2 DEVELOPMENT IN UTERO

In 1839 Schwann concluded that there is one general principle for the formation of all organisms: their make-up of cells. However, it took further two decades until Gegenbaur (1861) demonstrated that also the bird's ovum is a single cell. This single cell has some specific properties such as polarity that it gains during its descent along the mother's reproductive system by rotation.

After fertilization in the uppermost portion of the hen's oviduct the egg moves to the uterus where cleavage begins. The egg remains about 20 hours in the uterus before it is laid and undergoes further cleavage divisions forming a blastodisc. The cells in the center of the blastodisc are smaller than those in its periphery. The center of the disc is called area pellucida because of its translucent appearance. The outer, more opaque part of the blastoderm is known as the area opaca and the junctional region is referred to as the marginal zone. At the time when the egg is laid the blastoderm consists of about 60 000 cells. By the end of the uterine period, cells in the center of the blastoderm form an organized epithelium which later can be seen to be continuous over both, area opaca and area pellucida. They constitute a one cell thick layer that soon becomes pseudostratified and columnar (Fig. 12.1). From this layer a second layer of cells originates, the hypoblast. The upper layer of cells is now named the epiblast. The hypoblast cells originate from the area pellucida by ingression and from the posterior marginal zone by spreading and they are first arranged in several unconnected islands of 5-20 cells. These islands form the primary hypoblast. Later, when the cells form a continuous epithelium, this sheet is called secondary hypoblast. Hypoblast cells can be visualized by the monoclonal antibody HNK-1 (Canning and Stern 1988). The blastoderm now consists of two layers: the outer epiblast that gives rise to all of the embryonic tissues and the hypoblast forming the roof of the subgerminal cavity from which only extra-embryonic tissues will arise. The main function of the hypoblast is to control the development of the epiblast (Waddington 1932, 1933; Azar and Eyal-Giladi 1979; Eyal-Giladi 1984). The hypoblast, for instance, dictates the direction of the primitive streak and positions it by antagonizing nodal signaling (Bertocchini and Stern 2002).

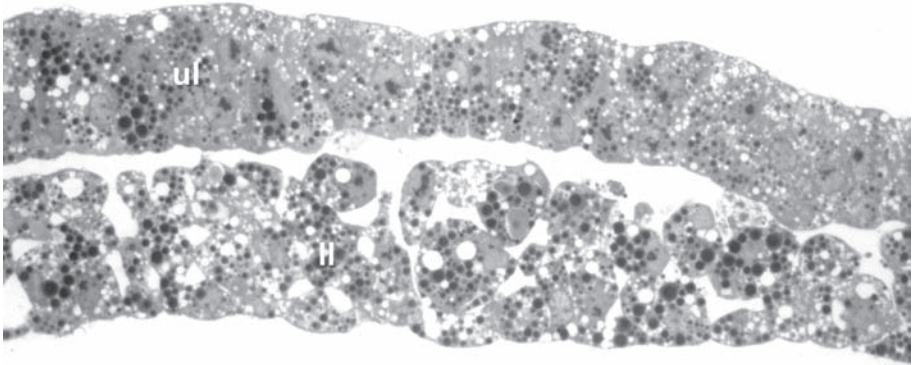


Fig. 12.1 Vertical section through the blastoderm of a chick embryo at the time of laying. Upper cell layer (epiblast, ul), developing lower cell layer (hypoblast, ll) and yolk droplets. Original.

12.3 GASTRULATION

A condensation of cells, the primitive streak, becomes visible at the posterior edge of the area pellucida. This structure elongates anteriorly until it reaches the center of the blastoderm. At its anterior end, a disc-shaped thickening of cells arises, the node, which is called after its discoverer Hensen's node (Fig. 12.2A). The term "node" was chosen by Hensen (1876) because in this area of the blastoderm the germ layers are tightly attached to each other as if being tied in a knot.

During gastrulation cells from the epiblast migrate into the streak and the node and pass through them to form the mesoderm and the endoderm (Fig. 12.2B,C). The streak cannot be regarded as a special growth zone, but rather as a location of cell movements where cells of the epiblast undergo an epithelio-mesenchymal transition in order to become able to migrate. According to Stern (1990) the cells of the epiblast do not invaginate through the midline of the primitive streak but through its lateral margins. In the midline of the streak, a cell population is situated that has its origin from the posterior marginal zone and does not contribute to the mesoderm.

Hensen's node is the source of the prechordal mesoderm, the head process, the notochord and the medial half of the paraxial mesoderm (Selleck and Stern 1992). After Spemann and Mangold (1924) had discovered the organizing function of the dorsal blastopore lip in amphibian embryos, Waddington and Schmidt (1933) presented experimental evidence that Hensen's node of the avian embryo has a capacity homologous to Spemann's organizer in amphibian embryos. The capacity includes the ability to induce a secondary embryonic axis with an ectopic nervous system in a host embryo.

Stern and his co-workers have studied in detail movements of cells towards and from Hensen's node during avian gastrulation and analyzed the molecular interactions involved (Selleck and Stern 1991, 1992; Psychoyos and

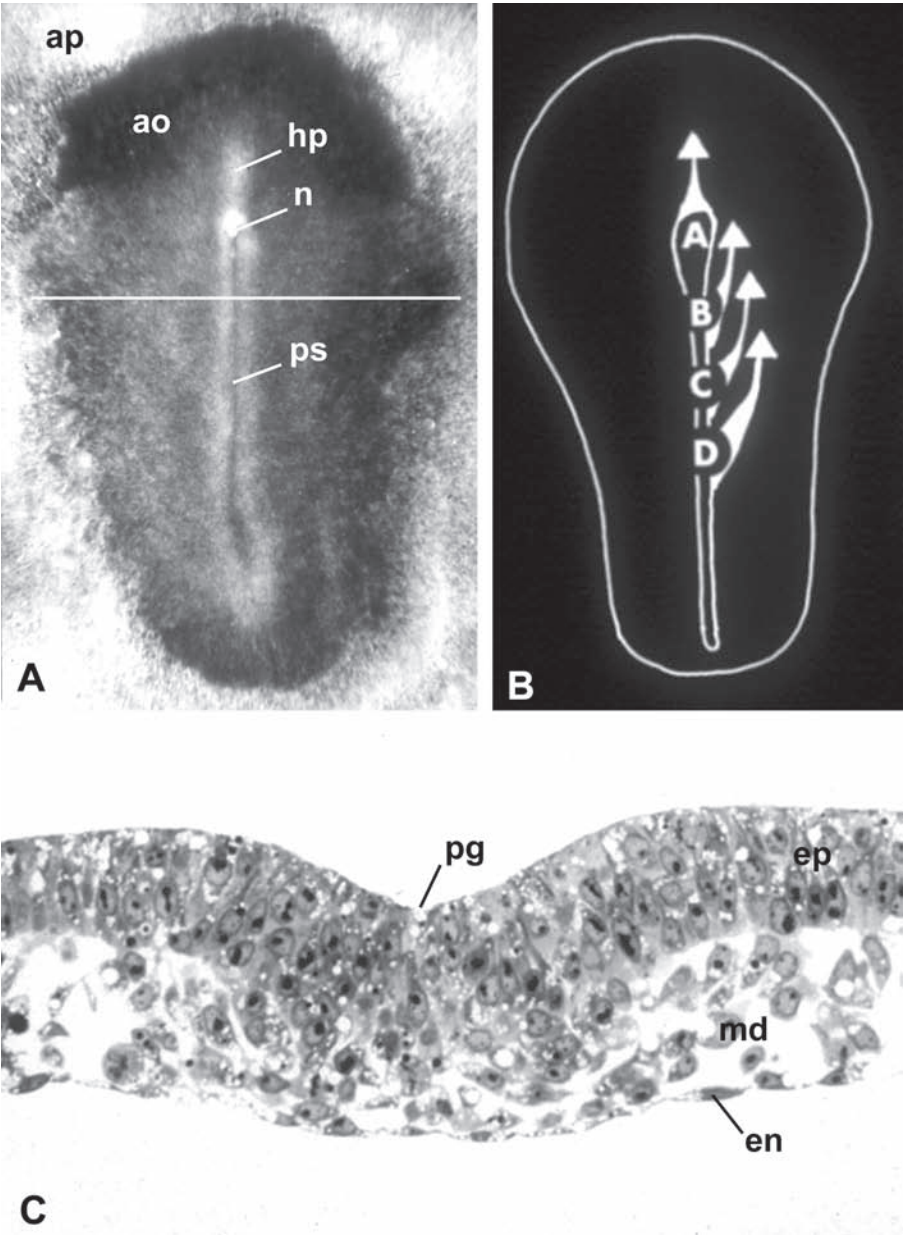


Fig. 12.2 HH-stage 5 chick embryo. **A.** Dorsal view, Area opaca (ao); Area pellucida (ap), head process (hp), Hensen's node (n), primitive streak (ps). Line indicates the section plane of C. **B.** Origin of definitive mesodermal compartments: notochord (A) paraxial mesoderm (B) intermediate mesoderm (C), lateral plate mesoderm (D). **C.** Transverse section, primitive groove (pg), epiblast (ep), endoderm (en), migrating mesodermal cells (md). Dorsal is to the top. Original.

Stern 1996a, 1996b; Joubin and Stern 1999, 2001). In addition, Hensen's node provides cells that form the definitive inner layer of the blastoderm, the endoderm. After removal of the node in stage 4 embryos (staging according to Hamburger and Hamilton, 1951), the node regenerates and a normal embryo develops suggesting that the node cannot be considered as a separate entity but rather represents a transitory functional structure formed by the blastoderm (Grabowski 1956; Psychoyos and Stern 1996a, 1996b).

The organizing function of the node can be visualized by the expression of a number of genes in a stage- and region-specific manner (Fig. 12.3). These include the homeobox genes *gooseoid* (Izpisua-Belmonte *et al.* 1993), *cNot* (Knezevic *et al.* 1995; Stein und Kessel 1995), and *Otx2* (Bally-Cuif *et al.* 1995) as well as the secreted factors HGF/SF (Streit *et al.* 1995), Sonic hedgehog (Shh) (Riddle *et al.* 1993; Roelink *et al.* 1994), Chordin (Streit *et al.* 1998), Dickkopf1 (Foley *et al.* 2000), Fgf8 (Crossley *et al.* 1996; Stolte *et al.* 2002), and the transcription factors Lim1 (Tsuhide *et al.* 1994) and HNF3b (Ruiz i Altea *et al.* 1995; reviewed by Lawson *et al.* 2001; Chapman *et al.* 2002).

Hensen's node has been found to play a crucial role in establishing left-right asymmetry (Levin *et al.* 1995). Several genes are expressed in or near the node in an asymmetric fashion (Levin *et al.* 1995, 1997; Collignon *et al.* 1996; Fig. 12.3B). These genes include *ActivinB*, *Shh*, *Fgf8*, *Caronte* (*car*) and *nodal* (reviewed by Pagán-Westphal and Tabin 1998; Capdevila *et al.* 2000; Rodriguez-Esteban *et al.* 2001). The laterality in organ formation, such as uni-directional looping of the heart and development of the gut, depends on the asymmetric expression of laterality genes that is preceded by an asymmetric morphology of the node and the cranial part of the primitive streak (Dathe *et al.* 2002). The right lip of the streak and the node is much more prominent than the left one and contains a cylindric cell condensation that is connected with the head process (Fig. 12.3C). A prerequisite for the development of left-right sidedness is the existence of a midline barrier that keeps cells and signals from crossing over to the contralateral side. This barrier has been identified to be the midline cells of the primitive streak and the notochord anterior to the node (Kelly *et al.* 2002; Klessinger and Christ 1996). The barrier function of the notochord was found to be mediated by Lefty1 that acts as a midline barrier molecule and is expressed in the notochord and the floor plate of the neural tube (Meno *et al.* 1998; Rodriguez Esteban *et al.* 1999).

Mesodermal cells originating from the primitive streak become situated in a characteristic distribution within the embryo proper. Those from the anterior-most part of the streak contribute to the paraxial mesoderm forming the lateral halves of the somites (Selleck and Stern 1992). The more posterior their origin, the more lateral is their location in the mesoderm of the embryo, meaning that the anterior-posterior axis of the primitive streak corresponds to the medio-lateral axis of the embryo (Fig. 12.2B).

As a result of gastrulation, four mesoderm compartments can be distinguished in a medial to lateral direction (Figs. 12.13, 12.15): 1. axial mesoderm (prechordal mesoderm, head process, notochord), 2. paraxial mesoderm (head

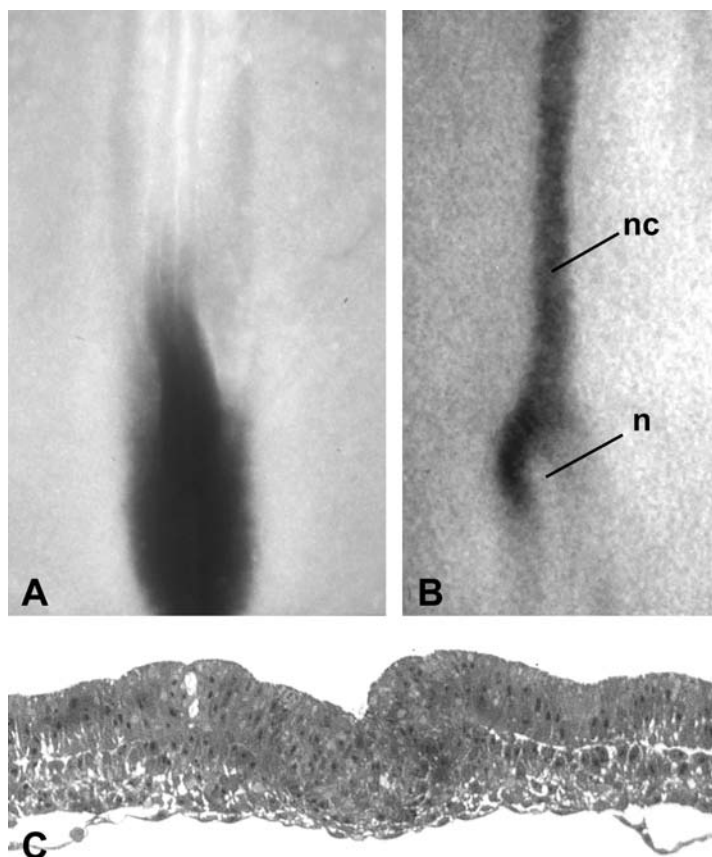


Fig. 12.3 **A.** Caudal end of an early embryo showing *Fgf8* expression in Hensen's node and caudal paraxial mesoderm. **B.** *Sonic hedgehog* (*Shh*) expression around Hensen's node (n) and in the notochord (nc). Note the asymmetric expression of *Shh*. **C.** Transverse section through Hensen's node. Note the asymmetry of the midline structures. Original.

mesoderm, somites) 3. intermediate mesoderm, 4. lateral plate mesoderm (somatic and splanchnic). The primordial germ cells appear at the extreme anterior edge of the area pellucida, outside the embryo proper.

During gastrulation, the embryo grows in a cranio-caudal direction by continuous addition of new material born in both the node and streak at its caudal end (Fig. 12.3A).

The primitive streak and node move backwards (regression of the primitive streak), as the head process and notochord elongate anterior to them (Fig. 12.2A). The shortening of the primitive streak occurs mainly at the posterior end from which cells spread out laterally and posteriorly to form extraembryonic mesoderm. The shortening continues until only the node and a bit of the streak caudal to it remains, at which point the tail fold is formed

and the node is incorporated in the tail bud that takes over the generation of new material. The part of the embryo cranial to the level of somite 27 or 28 is formed during the existence of the primitive streak (primary gastrulation), all structures of the embryo caudal to this level are added by the tail bud (secondary gastrulation).

The result of gastrulation is the rearrangement of the embryo to a stage characterized by the presence of three germ layers, ectoderm, mesoderm, and endoderm (Fig. 12.2C). One of the major consequences of this reorganization is that groups of cells reach their definitive position and come close enough together to undergo the inductive interactions that are involved in the establishment of the major organ systems.

12.3.1 Fate Maps of the Early Chick Embryo

Cell lineage tracing is a major interest in descriptive embryology. By following the developmental fate of individual cells, or little clusters of cells, from early developmental stages until later stages of differentiation, fate maps of the early embryo can be constructed. Fate maps depict the prospective fate of cells during normal development, but do not allow conclusions about the commitment of the cells. In chick, fate maps of the pre-primitive streak epiblast (Kopsch 1926; Gräper 1929; Wetzel 1929; Pasteels 1937) and the gastrulating embryo (Rosenquist 1966; Vakaet 1970; Nicolet 1971) have been elaborated by classical embryologists based on the use of e.g. localized cell destruction or labelling of cells by carbon particles and other staining techniques (reviewed in Schoenwolf 1991). With the introduction of a detailed staging table for pre-primitive streak stage chicken embryos (Eyal-Giladi and Kochav 1976) and the availability of an efficient marking technology using the fluorescent dyes DiI and DiO (Honig and Hume 1986) or CFSE (Garton and Schoenwolf 1996), detailed maps of the fate of chick epiblast cells became available. The general distribution of different prospective cell types in the avian epiblast is similar to that of other species such as zebrafish, frog and mouse. However, in early epiblastic maps prior to HH-stage 3, it became clear that in contrast to previous fate maps suggesting sharp borders between presumptive territories, there is a considerable overlap between different prospective areas (Hatada and Stern 1994). Moreover, the prospective areas are not stable, but change shape and position considerably including extensive cell mixing long before primitive streak formation, which marks the advent of gastrulation movements. Generally, between pre-gastrula stage X (Eyal-Giladi and Kochav 1976) and HH-stage 3, cells in the posterior half of the area pellucida tend to converge towards the midline and move anteriorly along the midline, thereby changing the relative position of prospective areas (Hatada and Stern 1994). Interestingly, while the majority of precursor cells is restricted to one side of the embryo, only presumptive somite cells seem to cross the midline during these movements. The pivot of gastrulation, Hensen's node, is likely to be of mixed origin, with contributions of gooseoid-positive cells from Koller's sickle and cells from the epiblast (Izpisua-Belmonte *et al.* 1993; Hatada and Stern 1994).

Figure 12.4 shows a fate map of a chicken embryo at intermediate primitive streak stage (HH-stage 3) (modified from Lopez-Sanchez *et al.* 2001). It is important to note that the boundaries of the prospective regions are not as sharp as suggested, but rather gradual and changing with development.

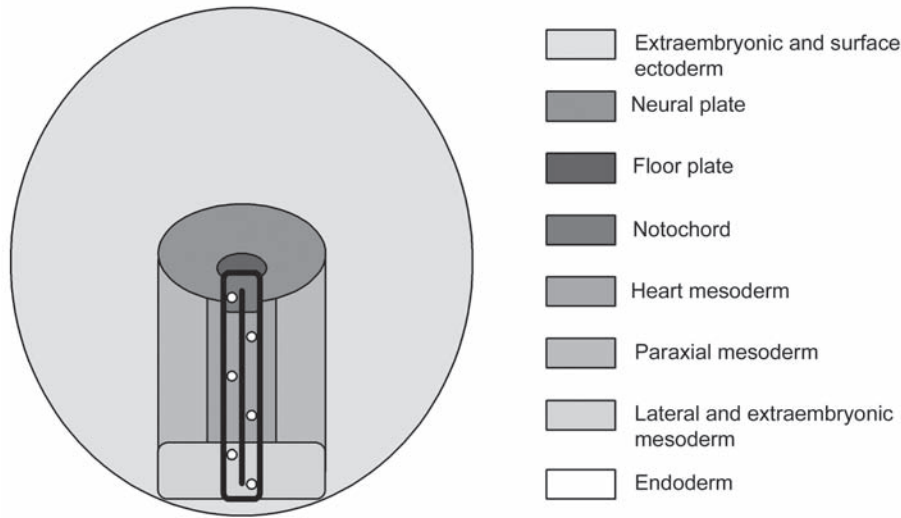


Fig. 12.4 Fate map of an intermediate streak stage embryo according to Lopez-Sanchez, C., Garcia-Martinez, V. and Schoenwolf, G.C. 2001. *Cells Tissues Organs* 169: 334-346, Fig. 6, modified.

The extraembryonic and surface ectoderm derives from the majority of the peripheral epiblast, outside a boundary at a distance of approximately 500 μm from the still elongating primitive streak. Within this boundary, the prospective neural plate is located in the area surrounding the cranial end of the primitive streak, in close association with the prospective neural inducer, Hensen's node. Within this prospective area, the future floorplate of the neural tube is restricted to the midline just anterior to the streak. During primitive streak progression, the floorplate precursors will become integrated into the anterior end of the streak. The notochord originates from cells within the cranialmost primitive streak. The intermediate section of the streak, and the adjacent epiblast cells at either side of the streak, give rise to the heart and associated blood vessels. At the same anteroposterior level, but lateral to the heart precursors, the prospective somite cells are flanking either side of the streak. In contrast to the distinct prospective domains of the ectodermal and mesodermal fates, the endoderm arises from cells from all levels of the intermediate primitive streak, but not from the epiblast outside the streak (Lopez-Sanchez *et al.* 2001).

12.4 BODY SHAPE AND EXTERNAL APPEARANCE

The early avian embryo is a flat disc, the blastoderm (Fig. 12.1). Its center is destined to form the embryo proper whereas its periphery gives rise to the yolk sac and amnion. The first intraembryonic structures appear with the formation of the head process in HH-stage 5 embryos. The head process and its continuation, the notochord, elongate whereas their source, Hensen's node, changes its position in a craniocaudal direction during the regression of the primitive streak. Cranial to the tip of the head process, a crescent-shape groove appears that marks the cranial boundary between embryonic and extraembryonic structures. The part of the blastoderm that is located caudally to this groove grows and rises above the flat blastoderm. This fold of the blastoderm includes the endoderm forming the foregut and represents the head rudiment. During further development the head expands further cranial and becomes progressively demarcated laterally from extraembryonic structures by forming the lateral head folds (Fig. 12.9). With the longitudinal growth of the embryo, its folding-off progresses and the lateral head folds are continued as lateral body folds (Fig. 12.5), and eventually as the tail fold. The folds include the ectoderm, somatic mesoderm, splanchnic mesoderm, and endoderm and demarcate the embryo from extraembryonic structures. At HH-stage 12, the head begins to bend ventrally forming the cranial flexure and to rotate so that its left side comes to lie against the yolk sac. Then, beginning at HH-stage 14, the cervical flexure occurs with a bending of the head in the neck region (Fig. 12.6). In addition, the trunk turns so that, at HH-stage 22, the whole embryo lies on its left side. The trunk itself becomes increasingly bent so that the tail bud approaches the head (Fig. 12.7A).

12.5 EXTRAEMBRYONIC MEMBRANES

The extraembryonic membranes include the yolk sac, the chorioallantois and the amnion. These structures are not part of the embryonic body proper and are discarded at hatching. The yolk sac is formed from the area opaca and initially consists of a thin ectoderm and an endodermal cell layer of which the cells contain many yolk droplets. Initially, the embryo lies flat on the yolk sac (Fig. 12.9). With the development of the body folds, which become progressively deeper, the embryo becomes separated from the yolk sac (Fig. 12.5).

The yolk sac is surrounded by the vitelline membrane, to which the periphery of the area opaca is attached using it as a substratum for cell migration. The migration takes place all around the periphery of the area opaca leading to a gradual expansion of the entire blastoderm.

The yolk sac becomes invaded by mesoderm cells which have ingressed through the posterior part of the primitive streak during gastrulation. These cells then migrate laterally to colonize the area opaca and express VEGFR2 (Nimmagadda *et al.* 2004). They begin to form blood islands and blood vessels under an inductive influence of the endoderm (Fig. 12.8). The vascularized region of the yolk sac is called the area vasculosa and separated from the

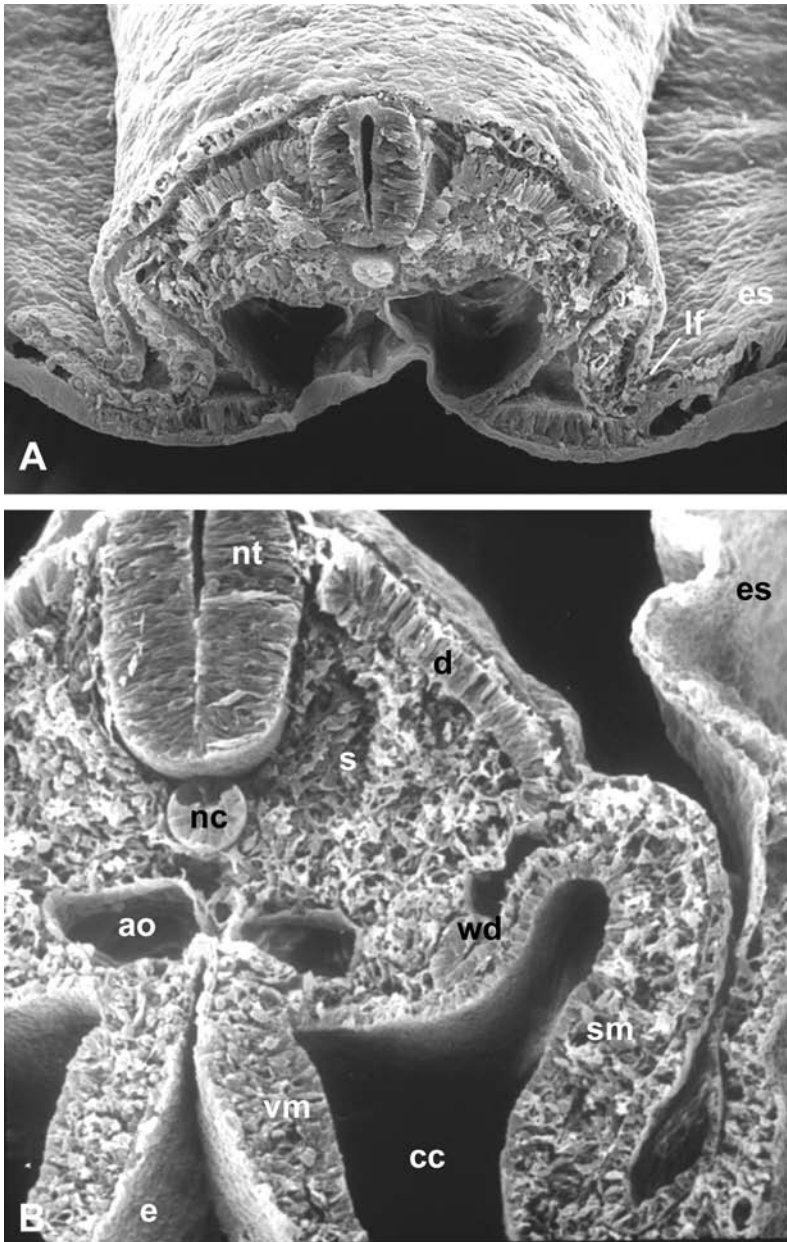


Fig. 12.5 Scanning electron micrographs of transverse fractures of 2-day chick embryos. **A.** Overview. Lateral body folds (lf) demarcate the embryo from extraembryonic structures (es). **B.** Higher magnification. Neural tube (nt), notochord (nc), dermomyotome (d), sclerotome (s), Wolffian duct (wd), endoderm (e), Visceral mesoderm (vm), somatic mesoderm (sm), coelomic cavity (cc), aorta (ao). Courtesy of Dr. H.J. Jacob, Bochum.



Fig. 12.6 Dorsal view of a HH-stage 14 embryo. Expression of *Pax1*. Note the flexure and rotation of the head. Original.

peripherally located area vitellina by the sinus terminalis. During the third day, the vitelline membrane breaks down over the embryo. After the embryo has become lifted up above the yolk sac by formation of the body folds, it remains connected with the yolk sac by the yolk sac stalk. The amnion and chorion are closely associated and arise together from the extraembryonic somatopleure. The first indication of the developing amnion is the appearance of the head fold of the amnion, a fold of the somatopleure anterior to the head.

The inner part of the folds will become the amnion whereas the outer will form the chorion. In HH-stage 13 embryos, the cephalic fold of the amnion envelops the head. During further development the whole embryo becomes covered by this double-walled pocket of extraembryonic somatopleure that caudally arises as lateral amniotic folds (Fig. 12.10) that grow together and eventually meet at the midline to form the amniotic raphe. The amnion lines the amniotic cavity and produces the amniotic fluid. The confined cavity between the amnion and chorion is the continuation of the extraembryonic coelom.

The chorioallantoic membrane is formed by a fusion of the chorion and the allantois. The allantois differs from the amnion and chorion in that it has an intraembryonic origin. It arises from the endoderm and the splanchnic mesoderm of the hindgut in the chick embryo at HH-stage 18. The growing

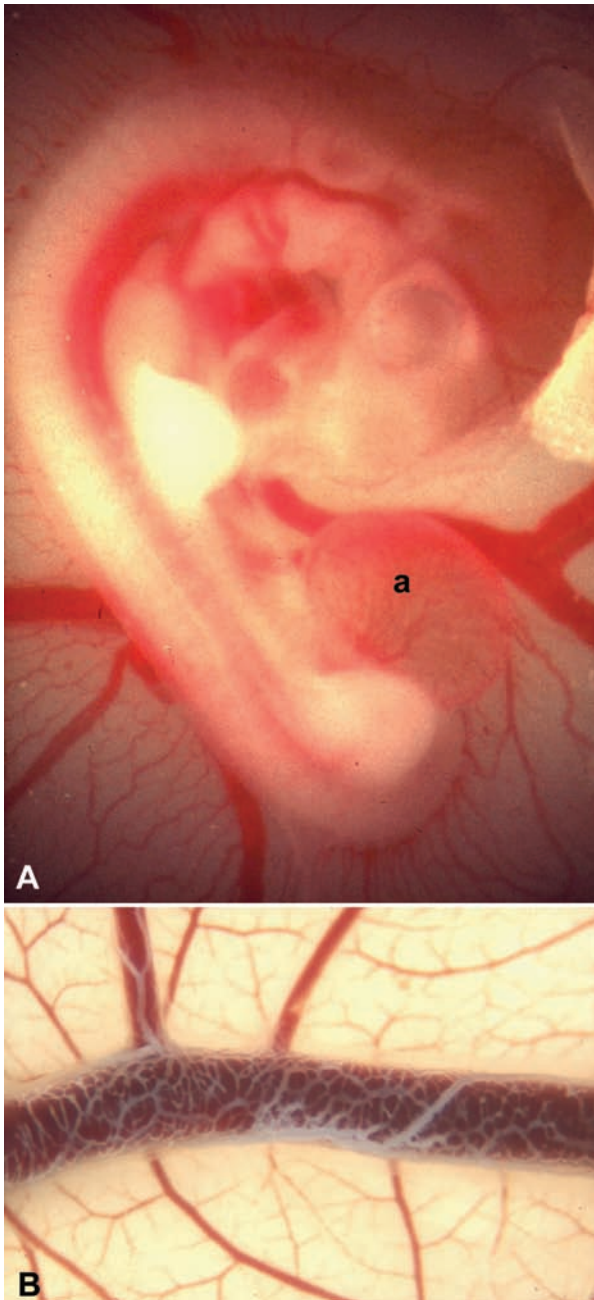


Fig. 12.7 A. Living 4-day embryo photographed *in ovo*. Note flexure of head and neck. Allantois (a). B. Differentiated chorioallantoic membrane (CAM) of a 13-day embryo. The lymphatic plexus around a larger vein is visualized by intralymphatic injection of Mercocox-blue. Courtesy of Dr. J. Wilting, Göttingen.

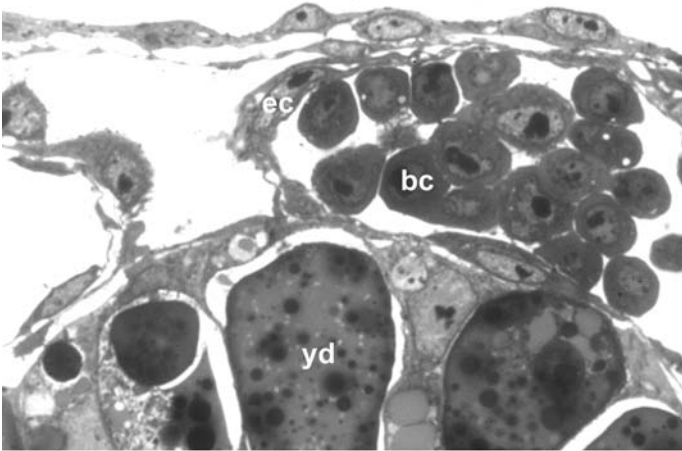


Fig. 12.8 Blood island of the yolk sac with peripheral endothelial cells (ec), and centrally located blood cell precursors (bc), yolk droplets (yd). Original.

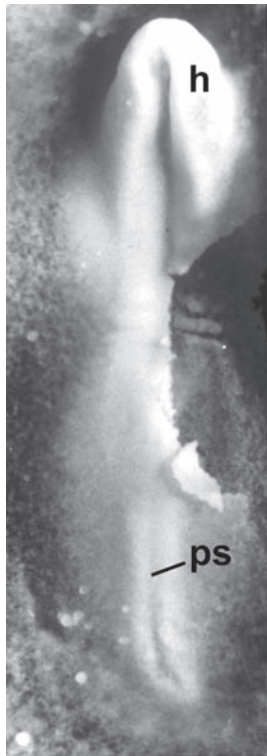


Fig. 12.9 Dorsal view of a HH-stage 7 embryo. Ectoderm is partially removed on the right side to show the first somites. Primitive streak (ps). The head (h) starts to elevate from the yolk sac. Original.

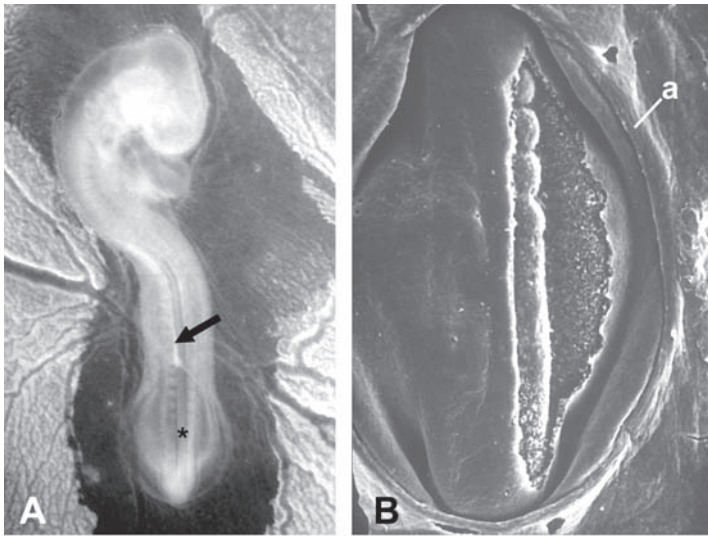


Fig. 12.10 **A.** 3-day embryo *in ovo* covered by the amnion except its caudalmost part (asterisk). Note the amniotic raphe (arrow). **B.** Scanning electron micrograph of the caudal part and the tail bud of a 3-day embryo. The ectoderm is partially removed on the right side to make the mesoderm visible. Note the margin of the amnion (a). Courtesy of Dr. H.J. Jacob, Bochum.

allantois leaves the intraembryonic coelom and enters the extraembryonic coelom forming the rapidly enlarging allantoic vesicle (Fig. 12.7A). The mesoderm of this balloon-like vesicle fuses with the mesoderm of the chorion forming the chorioallantoic membrane that consists of ectoderm from the chorion, mesoderm from both the chorion and allantois, and endoderm from the allantois. In the double layer of mesoderm an extremely rich vascular network develops which is connected with the intraembryonic circulation by the allantoic (umbilical) arteries and veins. Through the chorioallantoic membrane (Figs. 12.7B, 12.11) which is closely associated to the shell, the chick embryo takes up about 5 liters of oxygen and gives off about 4 liters of carbon dioxide during the 21-day period of incubation (Wangensteen 1972; Freeman and Vince 1978; Paganelli 1991). Further functions are the storage of waste products, including urea, uric acid and ammonia, as well as the absorption of calcium ions from the shell.

12.6 NEURULATION

After gastrulation, the future development of the germ layers depends on inductive interactions among some of these newly associated groups of cells. The primary inductive event in the embryo proper is the action of the chorda-mesoderm (head process and notochord) on the overlying ectoderm, resulting in the transformation of unspecialized ectodermal cells into the primordium

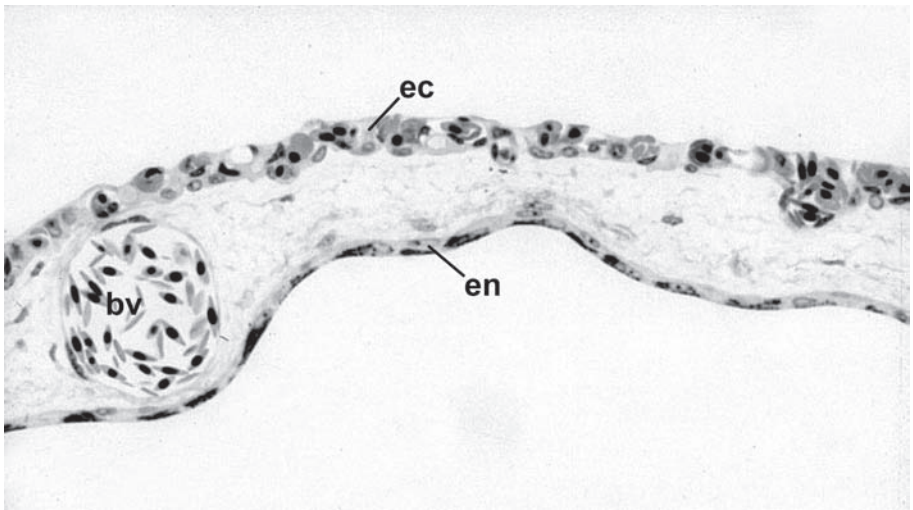


Fig. 12.11 Section of the chorioallantoic membrane consisting of the vascularized ectoderm (ec), blood vessels (bv) in the mesoderm, endoderm (en). Courtesy of Dr. J. Wilting, Göttingen.

of the nervous system, the neuroectoderm. The morphologically visible response of the induced ectoderm is to form a plate of thickened cells. Soon this plate becomes transformed in paired neural folds with a longitudinal groove in between. Ultimately, the two folds become elevated (Fig. 12.12) and eventually come together in the dorsal midline to form a complete neural tube. Closure of the neural tube first occurs at the upper spinal cord levels and from there it extends both rostrally and caudally in a zipper-like fashion. After

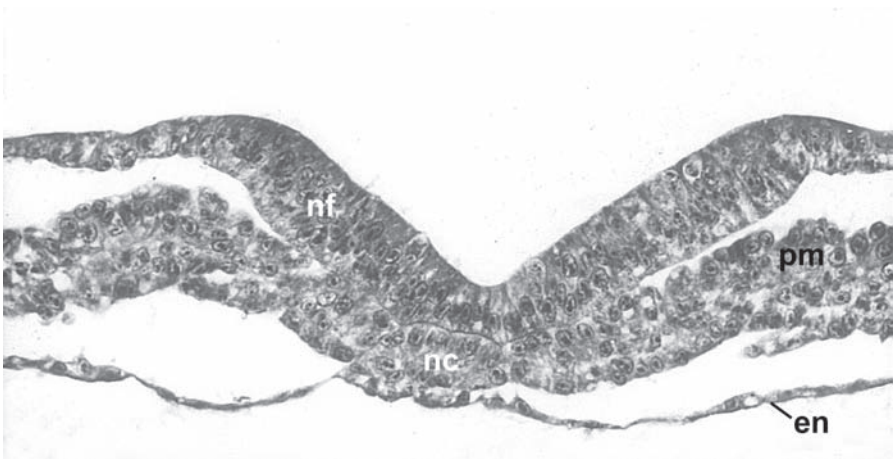


Fig. 12.12 Transverse section of a HH-stage 7 embryo at neural fold level. Neural folds (nf), notochord (nc), paraxial mesoderm (pm), endoderm (en). Original.

closure, the neural tube becomes covered by the ectoderm beyond the neural folds, now known as epidermis (Fig. 12.13). During and after neurulation there is a striking elongation of the body with the result that the whole trunk and tail region are derived from the posterior quarter of the neurula-stage embryo.

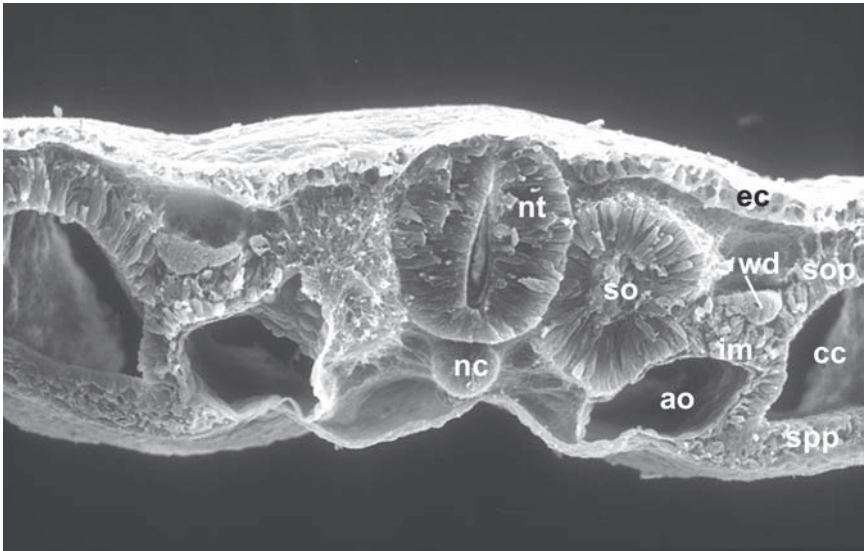


Fig. 12.13 Scanning electron micrograph of transverse fracture through a 2-day embryo. Ectoderm (ec), neural tube (nt), notochord (nc), somite (so), intermediate mesoderm (im) and Wolffian duct (wd), somatopleure (sop), splanchnopleure (spp), coelomic cavity (cc), aorta (ao). Courtesy of Dr. H.J. Jacob, Bochum.

The process of neural folding can be attributed to intrinsic changes in the shape of neuroepithelial cells. As these cells elongate their inner apices constrict. Elongation of cells requires intact microtubules running from the base to the apex of the cells and is accompanied by a contraction of thin microfilaments located just beneath the apical surfaces of the cells. In addition to these changes in cell shape, extrinsic influences are required for the formation of the neural tube as this morphogenetic process is the result of a number of factors acting in concert (Schoenwolf 1990). In the caudal part of the embryo, the neural tube is formed in a different manner that can be called secondary neurulation. It begins with the formation of a mesenchymal condensation beneath the dorsal ectoderm of the tail bud (Fig. 12.14). Through a process of cavitation and cell death, a central canal forms directly (Schoenwolf 1977, 1979). This central canal becomes continuous with the central canal of the primary neural tube.

Neural induction is mediated by inhibitors of BMPs (bone morphogenetic proteins) secreted by the chorda-mesoderm. First hints to this mechanism came from the disaggregation of *Xenopus* gastrula ectoderm and culture at low

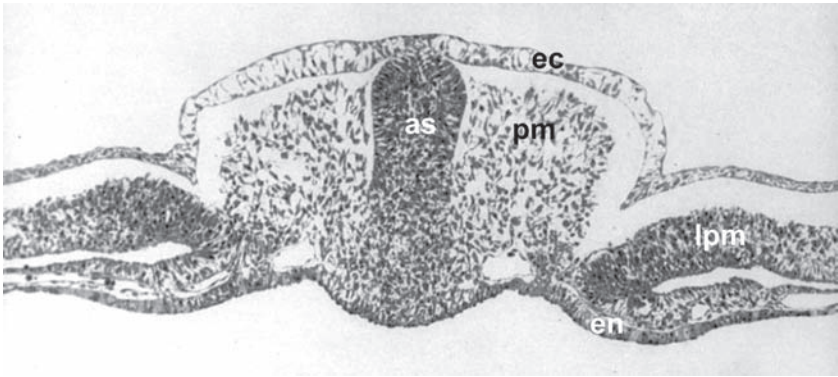


Fig. 12.14 Transverse section through a tail bud of a 3-day embryo. In the center, the cells undergo a mesenchyme-to-epithelium transition to form the axial structures (as). Paraxial mesoderm (pm), ectoderm (ec), endoderm (en), lateral plate mesoderm (lpm). Original.

cell density (Grunz and Tacke 1989). Growth factors secreted by the disaggregated cells are no longer retained in the extracellular matrix near the cells but are diluted into the culture medium. Under these experimental conditions the ectodermal cells become committed to a neural fate. This led to the suggestion that neuralization can arise from the removal of an inhibitory substance (Hemmati-Brivanlou and Melton 1994). It has been shown that the same signals are responsible for both, dorsalization of the mesoderm leading to the specification of the paraxial mesoderm and for neural induction. Three substances secreted by the organizer region, noggin, follistatin and chordin, are inhibitors of BMPs. BMP4 is produced by the embryo in all regions except those affected by the activation of the Wnt pathway. The three BMP inhibitors act by direct binding to and inhibition of BMP protein (Sasai and De Robertis 1997). This means that there is a gradient of BMP activity from lateral (ventral) to medial (dorsal). It has been shown that the *vent1* gene is activated at high BMP concentration and the *vent2* gene at low BMP concentration. The proteins coded by these genes are themselves transcriptional repressors. The domain of the mesoderm in which both *vent* genes are expressed becomes the lateral plate whereas the domain in which only *vent2* is on becomes the paraxial mesoderm.

Anterior-posterior patterning of the embryo is controlled by different signals. The anterior part is characterized by the expression of genes coding for transcription factors including *gooseoid* that induces anterior type genes such as *otx2* (reviewed in Boettger *et al.* 2001; Niehrs 2005).

12.6.1 The Neural Crest

The neural crest is a population of cells derived from the neural folds. After their fusion, neural crest cells begin to emerge from the dorsal part of the neural tube and then migrate away into the surrounding tissues (Fig. 12.15). Neural crest cells form a variety of different cell types including neurons and

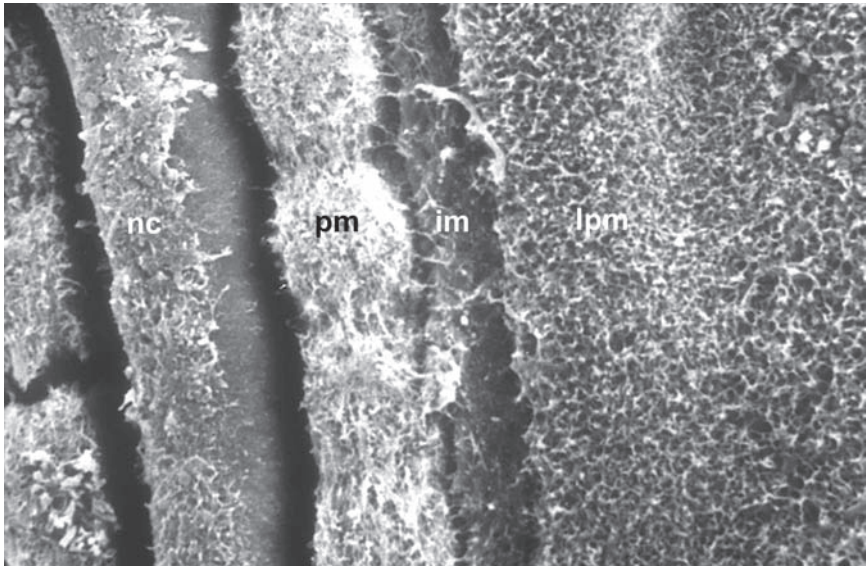


Fig. 12.15 Scanning electron microscopic dorsal view on a 2-day chick embryo after ectoderm removal. Neural crest cells (nc) on the neural tube, paraxial mesoderm (pm), intermediate mesoderm (im), lateral plate mesoderm (lpm). Courtesy of Dr. H.J. Jacob, Bochum.

glia of the sensory and autonomic systems, Schwann cells, adrenal medulla, pigment cells, and in the head connective and skeletal tissues as well as smooth muscle. As a prerequisite for migration the neural crest cells undergo an epithelial-to-mesenchymal transition and stop expression of N-cadherin (reviewed in Nieto *et al.* 2001; Derycke and Bracke 2004). The crest cells express *Slug*, a zincfinger transcription factor. Ablation of the *slug* m-RNA by antisense treatment can prevent neural crest migration and differentiation (Carl *et al.* 1999). The neural crest cells become progressively committed by their location (head and trunk), their timepoint of birth and the environment through which they migrate. Cultured trunk crest cells will preferentially form Schwann cells when exposed to neuregulin, smooth muscle cells when exposed to TGF β and autonomic neurons when exposed to BMP2 or BMP4. The trunk crest shows two distinct pathways of migration. The dorsolateral pathway is between the somite and the surface ectoderm and is used by melanocytes. The ventral pathway through the sclerotome is used by cells that give rise to the dorsal root ganglia, the sympathetic nervous system, the adrenal medulla, and make contribution to the heart.

12.7 SEGMENTATION OF THE PARAXIAL MESODERM: FORMATION AND DIFFERENTIATION OF SOMITES

Mesoderm originates from cells derived from the epithelial epiblast layer during gastrulation. These cells pass through Hensen's node and the

primitive streak and spread outward forming the definitive mesoderm (Fig. 12.2). The embryonic mesoderm is subdivided in medial-to-lateral direction into the axial, paraxial, intermediate and lateral plate mesoderm (Figs. 12.13, 12.15). Only the paraxial mesoderm undergoes segmentation and forms somites, except its cranial part which is located rostral to the otic placode.

12.7.1 Somite Formation

The trunk paraxial mesoderm becomes subdivided into segmental units, the somites, which are formed progressively in rostral-to-caudal direction (Fig. 12.16). The morphologically still unsegmented caudal part of the paraxial mesoderm, which is called segmental plate or presomitic mesoderm, becomes permanently supplemented at its caudal end by the incorporation of new cells arising in the course of gastrulation (Christ *et al.* 1998). Once formed, the continued viability of paraxial mesoderm depends on the presence of axial structures. If the segmental plate or early somites are removed from the embryo and cultured *in vitro* (Cann *et al.* 1999) or separated from the axial structures or surface ectoderm (Schmidt *et al.* 1998; Borycki *et al.* 1999), an increase of apoptosis and a decrease of cell proliferation within this mesodermal domain can be seen (Rong *et al.* 1992; Teillet *et al.* 1998). The segmental plate extends from Hensen's node, or tail bud, to the most recently formed somite and is

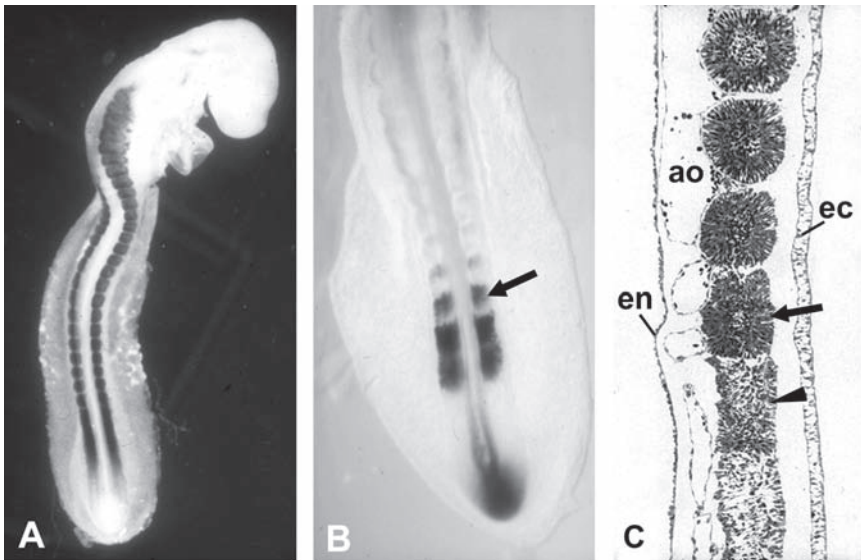


Fig. 12.16 Epithelialization and somite formation of the paraxial mesoderm in 2-day embryo. **A.** Expression of the epithelialization gene *paraxis*. Courtesy of Dr. D. Sosis, Dallas. **B.** Expression of *EphA4* in the region of somite formation. Arrow: somite I. Courtesy of Dr. C. Schmidt, London. **C.** Sagittal semithin section. Ectoderm (ec), endoderm (en), aorta (ao). Arrow: somite I. Arrowhead: somite in *statu nascendi*. Original.

characterized by an increasing maturation in a caudal-to-rostral direction. Caudally, it is made up of a loosely arranged mesenchyme. In the rostral segmental plate, cells become densely packed and polarized with the exception of centrally located cells that will reside in the somitocoele of the somites (Figs. 12.13, 12.16C). Somite formation occurs at the rostral end of the segmental plate and is characterized by a mesenchymal-to-epithelial transition of cells and the formation of boundaries (reviewed by Christ and Ordahl 1995; Gossler and Hrabé de Angelis 1998).

Prior to overt segmentation, a metameric arrangement of mesenchymal cells within the segmental plate can be visualized by stereoscaning electron microscopy (Packard 1980; Meier and Jacobson 1982). These metameric clusters, called somitomeres, are constant in number for a given species throughout the primary phase of somitogenesis. In the chick and quail, 10-12 somitomeres have been described (Packard 1978). It is suggested that somitomeres are precursors of the somites, appearing as bilateral pairs with the caudal-most pair located close to Hensen's node (Jacobson 1988). The existence of a metameric prepatterning in the segmental plate has also been demonstrated in isolation experiments where portions of the segmental plate underwent overt segmentation outside the normal embryonic environment (Christ *et al.*, 1972; Packard 1980).

The maturation of the segmental plate is accompanied by the expression of several genes. The cells of the loosely arranged mesenchyme in the caudal part of the segmental plate are characterized by the expression of *Fgf8* (Crossley and Martin 1995; Stolte *et al.* 2002; Fig. 12.3A). In the mid portion of the segmental plate, where the cells become polarized, *Paraxis*, a basic helix-loop-helix transcription factor, is expressed (Burgess *et al.* 1996; Fig. 12.16A). This factor has been found to be required for epithelialization of the cells in the segmental plate and somite formation. *Paraxis* expression is induced by *Wnt6* secreted by the surface ectoderm (Rodriguez-Niedenführ *et al.* 2003; Schmidt *et al.* 2004). Genes of the Notch and Eph signaling pathways are also involved in epithelialization and boundary formation (Hrabé de Angelis *et al.* 1997; Araujo and Nieto 1997; Palmeirim *et al.* 1998). Members of the Eph family of receptor tyrosine kinases and their ligands, the ephrins, are expressed in the paraxial mesoderm where they play a role in patterning the somite boundaries (Bergemann *et al.* 1995; Scales *et al.* 1995; Flenniken *et al.* 1996; Gale *et al.* 1996; Durbin *et al.* 1998; Schmidt *et al.* 2001; Fig. 12.16B).

12.7.1.1 Molecular basis of segmentation

As first postulated by Cooke and Zeeman (1976), a molecular clock controls oscillating patterns of gene expression within the segmental plate and produces periodicity within cells destined for somite formation (reviewed by Pourquié 2000). This oscillating gene expression is essential for segmentation of the segmental plate (Palmeirim *et al.* 1997, 1998). In the chick, expression of *c-hairy1*, *c-hairy2* and *lunatic fringe* rises and falls in a temporal-spatial periodic pattern (McGrew *et al.* 1998; Forsberg *et al.* 1998; Aulehla and Johnson

1999). These segmentation genes have modifying effects on the Delta-Notch signaling pathway in a way that Notch becomes activated along a boundary between cells that express *lunatic fringe* and cells that do not express this gene (Hrabé de Angelis *et al.* 1997; Irvine 1999). The cranio-caudal sequence of segmentation as well as the coordination within the segmental plates of both sides is controlled by a gradient of Wnt3a with the highest concentration being at the tail bud. The generation of segments depends on a cyclic expression of *Axin2* which is a target gene of Wnt3a and an inhibitor of the canonical Wnt pathway. As a consequence of alternate switching on and off of the Wnt signals, the Delta-Notch activity becomes modulated (Aulehla *et al.* 2003). This leads to changes of cell adhesion which is mediated by ephrins (Bergemann *et al.* 1995; Schmidt *et al.* 2001; Fig. 12.22). Additionally, the segments become subdivided in a rostral and caudal half which is morphologically visible in later stages. This polarization of prospective somites is caused by the Delta-Notch signaling pathway.

12.7.1.2 Somite nomenclature

In the old literature (e.g. Remak 1850) the somites were called protovertebrae because they are the forerunners of the vertebrae. The term “somite” was introduced by Balfour (1881) taking into account that these segmental units give not only rise to vertebrae but also to muscle and dermis. The first detailed description of early somite compartments was given by Williams (1910) who distinguished between dermatome, myotome and sclerotome. He followed Hatchesek (1880) who corrected the assumption by His (1868) that the ventral part of the somite only contributes to the formation of the aortic wall. Christ and Ordahl (1995) suggested replacement of the term “dermatome” by “dermomyotome” because this subdomain continues to give rise to both muscle and dermis as long as it exists (Scaal and Christ 2004).

Somites are formed from the cranial end of the segmental plate and mature along the longitudinal axis in caudal to cranial direction (Fig. 12.23). As a consequence, at every stage of development, embryos contain somites of differing stages of maturity. The total number of somite pairs is one of the most important criteria to exactly stage early avian embryos (Hamburger and Hamilton 1951). This means that every embryo with e.g. 19 somites (HH-stage 13), is at the same point in its development. However, when a HH-stage 13 embryo is compared to embryos of other developmental stages, it can be found that corresponding somites (e.g. the recently formed ones) are different in their states of maturity (Borman and Yorde 1994). Christ and Ordahl (1995) proposed a numbering system that takes into consideration both the maturation of the somite and the developmental stage of the embryo. In this system, the developmental age of the somite is denoted by Roman numbers, the caudal-most somite being number I. Prospective somites within the segmental plate are denoted by minus numbers. In this nomenclature, for instance, the fifth most recently formed somite of a HH-stage 13 embryo (an embryo with 19 somites) would be V/19.

12.7.2 Somite Maturation

The most recently formed somite is an epithelial sphere whose initially columnar epithelial cells surround a core of mesenchymal somitocoele cells (Figs. 12.13, 12.16C). Each somite is covered by a basal lamina that connects the somite with the adjacent structures by extracellular material: dorsally with the surface ectoderm, medially with the neural tube and notochord, and ventrally with the endoderm and aorta. Laterally, the somite is in continuous contact with cells of the intermediate mesoderm.

The subdivision of the somite into sclerotome, dermomyotome, and myotome depends on interactions with the surrounding tissues. If the recently formed somites are rotated such that the dorsal and ventral positions are reversed, or if the dorsal half of a somite is replaced by a ventral half, somite derivatives form normally in accordance with their new environment (Aoyama and Asomoto 1988; Christ *et al.* 1992). These results suggest that cells in the dorsal and ventral halves of the rotated somite are respecified. Additional experiments have shown that the medial and lateral somite halves are also subject to respecification (Ordahl and Le Douarin 1992).

12.7.2.1 Sclerotome

The first and most striking morphological characteristic of sclerotome formation in the avian embryo is an epithelio-mesenchymal transition (EMT) of the ventromedial half of the somite (Christ *et al.* 2004; Fig. 12.5A). Initiation and maintenance of the sclerotome depends on both Sonic hedgehog (Shh) and Noggin, a BMP4 antagonist, which are both expressed in the notochord when the sclerotome is forming (Fan and Tessier-Lavigne 1994; Johnson *et al.* 1994; Fan *et al.* 1995; Marti *et al.* 1995; Müller *et al.* 1996; McMahon *et al.* 1998). EMT in the ventromedial somitic wall is accompanied by down-regulation of N-cadherin which leads to a decrease in cell adhesion and an increase in cell motility (Hatta *et al.* 1987; Duband *et al.* 1987; Takeichi 1988).

The sclerotome is defined not only by its mesenchymal organization but also by the expression of sclerotome-specific marker genes, such as *Pax1* and *Pax9* (Dietrich *et al.* 1993, 1997; Koseki *et al.* 1993; Peters *et al.* 1995; Figs. 12.6, 12.17A). These genes form one group within the family of nine vertebrate *Pax* genes, which are characterized by the paired box that encodes a DNA-binding domain (Walther *et al.* 1991; Noll 1993). *Pax1* has been found to be already expressed in the ventromedial cells of the still epithelial somite (Deutsch *et al.* 1988; Ebensperger *et al.* 1995; Borycki *et al.* 1997; Balling *et al.* 1996; Müller *et al.* 1996). In the avian embryo, *Pax1* expression precedes the EMT, whereas *Pax9* expression cannot be seen until sclerotomal mesenchyme has actually formed (Müller *et al.* 1996). After experimental removal of the notochord prior to neural tube patterning, the acquisition of *Pax1* positivity in the ventral part of the somite is lost (Ebensperger *et al.* 1995). Both Shh and Noggin can induce *Pax1* and are suggested to cooperate during sclerotome formation (McMahon *et al.* 1998).

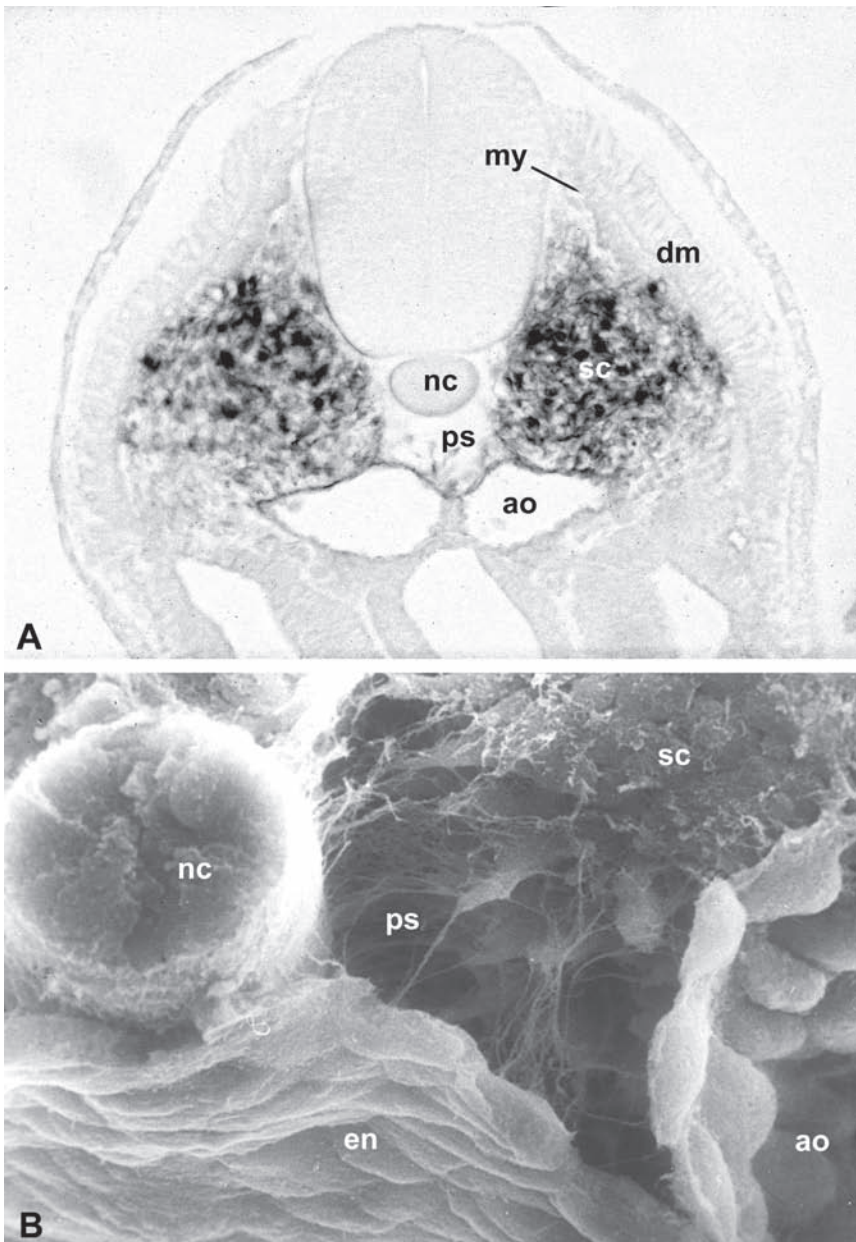


Fig. 12.17 Somite compartmentalization in a 2-day chick embryo. **A.** Transverse section showing *Pax1* expression in the sclerotome (sc). Dermomyotome (dm), epaxial myotome (my), perinotochordal space (ps). Original. **B.** Scanning electron micrograph showing sclerotomal cells (sc) invading the perinotochordal space (ps). Endoderm (en), notochord (nc), aorta (ao). Courtesy of Dr. H.J. Jacob, Bochum.

The size of the sclerotome is a result of the balance between dorsal and ventral signals. Dorsal signals promote the development of the dorsally located dermomyotome and suppress sclerotome formation (Ikeya and Takada 1998; Olivera-Martinez *et al.* 2001; Wagner *et al.* 2000). The dorsalizing signals are produced by the dorsal neural tube and surface ectoderm, and are mediated by the Wnt family of signaling molecules and their receptors (Hoang *et al.* 1998; Cauthen *et al.* 2001). *Wnt1* and *Wnt3a* are expressed in the dorsal neural tube and *Wnt6* in the ectoderm (Ikeya and Takada 1998; Capdevila *et al.* 1998; Cauthen *et al.* 2001; Schubert *et al.* 2002; Rodriguez-Niedenführ *et al.* 2003). *Wnt1*, -3a and -4-producing cells ectopically grafted between axial structures and somites induce an expansion of the dorsal somite compartment, the dermomyotome, at the expense of the ventral compartment, the sclerotome, which is reduced in size and characterized by a downregulation of *Pax1* (Wagner *et al.* 2000). On the other hand, transplantation of the notochord which is the source of ventralizing signals, into the dorsal somite domain leads to an expansion of the sclerotome at the expense of the dermomyotome (Brand-Saberi *et al.* 1993).

Within the sclerotome, different subdomains can be characterized by their vicinity to other structures, specific expression domains of genes, and their derivatives. The central sclerotome that is closely associated to the dermomyotome and later to the myotome gives rise to the pedicles, the ventral parts of the neural arches and the proximal ribs (reviewed by Christ *et al.* 2004). The ventral sclerotome is formed by the invasion of *Pax1* expressing cells from the ventromedial edge of the central sclerotome. These cells migrate into the perinotochordal space which is initially free of cells (Fig. 12.17). ECM material connects sclerotomal cells with the basement membrane of the notochord and functions as a substrate for invading cells (Jacob *et al.* 1975). The cells proliferate and form the perinotochordal tube from which vertebral bodies and intervertebral discs develop (Hall 1977; Christ and Wilting 1992; Christ *et al.* 2000). The dorsal sclerotome gives rise to the dorsal parts of the neural arches and to the spinous processes (Fig. 12.18). Its cells do not maintain expression of *Pax1* (Ebensperger *et al.* 1995) because of a negative effect of BMP4 that is produced by the roof plate of the neural tube and the surface ectoderm (Watanabe and Le Douarin 1996; Monsoro-Burq *et al.* 1996). These cells express *Msx1* and *Msx2* as soon as they become dorsally situated. These genes inhibit a premature differentiation of the cells which have to reach their destination between the roof plate of the neural tube and the surface ectoderm before chondrification starts. An additional subdomain of the sclerotome can be identified close to the lateral surface of the neural tube. It gives rise to blood vessels that invade the neural tube and to the meninges of the spinal cord (Christ *et al.* 2000; Halata *et al.* 1990; Nimmagadda *et al.* 2004, 2005). Cells of the lateral sclerotome down-regulate *Pax1* due to BMP4 signaling from the lateral plate mesoderm (Ebensperger *et al.* 1995). Their further differentiation to distal ribs and tendons depends on FGF-signaling from the myotome (Huang *et al.* 2003; Brent *et al.* 2003). Additionally, cells of the lateral sclerotome

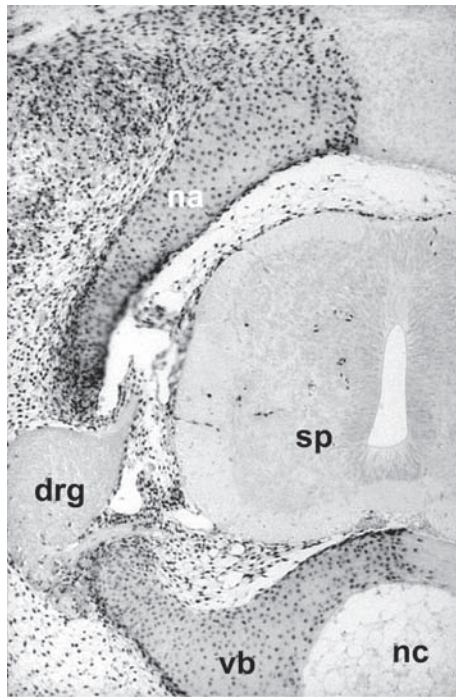


Fig. 12.18 Transverse section of a 8-day chick embryo after quail-to-chick transplantation of an epithelial somite. Graft-derived cells are stained with a quail-specific antibody. Spinal cord (sp), notochord (nc), dorsal root ganglion (drg), vertebral body (vb), neural arch (na). Original.

express *VEGFR2* under the control of *BMP4* and are destined to differentiate into endothelial cells and to form blood vessels (Wilting *et al.*, 1995; Eichmann *et al.* 1993; Nimmagadda *et al.* 2004, 2005).

As mentioned earlier, each segment becomes polarized in a cranio-caudal direction before the somite is formed. After somite compartmentalization, this subdivision is morphologically visible in the sclerotome and has important development consequences (Remak 1850; Brand-Saberi and Christ 2000; Fig. 12.19). On the one hand, it is the prerequisite for the “resegmentation” of the vertebral column. On the other hand, it causes the segmentation of the peripheral nervous system.

The present view of resegmentation in the avian embryo is based on studies by Bagnall *et al.* (1988, 1989), Huang *et al.* (1994, 1996, 2000), Ewan and Everett (1992), Aoyama and Asamoto (2000) and Evans (2003). According to this work, each vertebral body is formed by fusion of the caudal half of one sclerotome with the cranial half of the caudally adjacent sclerotome. This is also true for the rib with the exception of its head, neck, and distal-most part. The intervertebral disc originates from the somitocoele-derived cells, which, after somite compartmentalization, are located in the cranial part of the

caudal half-segment (Huang *et al.* 1994, 1996; Mittapalli *et al.* 2005). As a result of resegmentation, each segmental muscle is attached by its tendons to two adjacent vertebrae overspanning the movable intervertebral structures like discs, joints and ligaments.

Both halves of the sclerotome differ with respect to density and properties of cells (Fig. 12.30). Neural crest cells and axons invade only the cranial half of the sclerotome whereas the caudal half has a repellent influence on them (Keynes and Stern 1984; Rickmann *et al.* 1985; Bronner-Fraser 1986; Teillet *et al.* 1987).

Ephrins have been shown to be responsible for the repellent property of the caudal half-sclerotome. In the chick embryo, *EphrinB1* and *B4* are expressed in the caudal sclerotome and repel motor axons (Wang and Anderson 1997). Corresponding receptors for the ephrins, *EphB2* and *EphB3*, are present on the motoneuron axons restricting their outgrowth to the cranial half-sclerotome (Henkemeyer *et al.* 1994; Ohta *et al.* 1996; Robinson *et al.* 1997).

After invasion of the cranial sclerotome-half by neural crest cells and axons, the mesoderm cells which are, in contrast to their caudal counterparts, rather loosely packed, express cytotactin (Tan *et al.* 1987), tenascin (Mackie *et al.* 1988), and show butyrylcholinesterase activity (Layer *et al.* 1988), suggesting that there must be an interaction between sclerotomal cells on the one hand, and axons as well as neural crest cells on the other hand. In addition to these interactions, sclerotomal cells contribute to the spinal nerves by formation of perineurium and endoneurium as well as to connective tissue inside and outside the dorsal root ganglia (Halata *et al.* 1990).

Regarding the formation of sclerotomal subdomains in the dorsoventral and mediolateral direction and their contribution to the vertebrae, the process of vertebra development is becoming more complex with regard to the craniocaudal subdivision of the sclerotome and the role of these halves during resegmentation. The caudal half-sclerotome, for example, is characterized by the expression of the homeobox gene *Uncx4.1* (Fig. 12.19C). In homozygous *Uncx4.1* mutant mice, the pedicles, proximal ribs and transverse processes of the vertebrae are lacking indicating that both halves of the sclerotome differ with respect to their function in vertebra formation (Mansouri *et al.* 2000; Leitges *et al.* 2000; Schrögle *et al.* 2004).

Chondrogenic differentiation of sclerotomal cells depends on the expression of the homeobox gene *Bapx1* (Murtaugh *et al.* 1999, 2001). It has been shown that Meox proteins are required for *Bapx1* expression (Rodrigo *et al.* 2004) and that *Bapx1* is a direct target of *Pax1* and *Pax9* (Rodrigo *et al.* 2003). Shh establishes a *Bpx1/Sox9* autoregulatory loop that is maintained by BMP signals to induce chondrogenesis (Zeng *et al.* 2002). Other genes that are required for chondrogenic differentiation and that are expressed under the control of *Pax1* and *Pax9* are *Col2a1* encoding collagen II and its transcriptional activator *Sox9* (Bell *et al.* 1997; Healy *et al.* 1996; Bi *et al.* 2001).

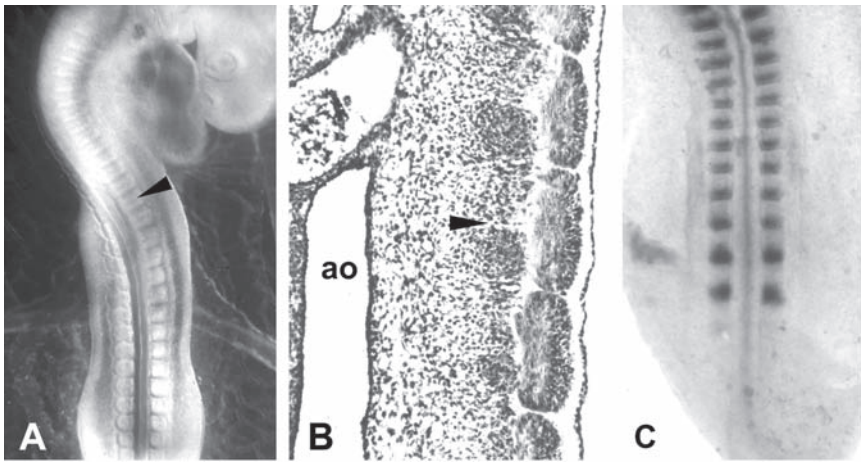


Fig. 12.19 A. Cranio-caudal polarization of the sclerotomes. Intervertebral (von Ebner's) fissures: arrowheads. A. Dorsal view of a 3-day embryo. B. Sagittal section. Aorta (ao). C. Dorsal view of a 2-day embryo showing expression of *Uncx4.1* in the caudal half-sclerotomes. Original.

12.7.2.2 Axial identity of somite derivatives

Vertebrae at different levels show distinct morphological features allowing discrimination, for instance, between cervical and thoracic vertebrae. This segment specificity has already become determined in the presomitic mesoderm. After heterotopic grafting of presomitic mesoderm from the prospective thoracic region into cervical or lumbosacral regions, ectopic ribs develop (Kieny *et al.* 1972; Jacob *et al.* 1975). On the other hand, cervical somites grafted into the thoracic region fail to develop ribs. This segment-specific identity is achieved by the function of the *Hox* gene family. In the avian embryo as in other higher vertebrates, four clusters of *Hox* genes can be distinguished (*HoxA*, *HoxB*, *HoxC*, and *HoxD*) which are located on different chromosomes. The single *Hox* genes of the *Hox* complexes are activated according to their serial arrangement within the *Hox* complex, a phenomenon that has been called "colinearity" (Duboule and Dollé 1989; Graham *et al.* 1989; Krumlauf 1994). It is suggested that transcriptional activation of *Hox* genes according to this colinearity is responsible for the development of axial identities of somite derivatives. Gruss and Kessel (1991) and Kessel (1991) have proposed the *Hox* code model that is characterized by a segment-specific combination of *Hox* gene expression that controls axial identities. Alterations of the *Hox* code change the segment identities resulting in the formation of segment-atypical vertebrae, a phenomenon that is called homeotic transformation. For instance, in gain-of-function mutant mice with ectopic expression of *Hoxd-4*, the occipital bone and atlas gained segmental identities characteristic of more caudal cervical vertebrae (Lufkin *et al.* 1992; Kessel *et al.* 1990).

12.7.2.3 Dermomyotome

After sclerotome formation by an epithelio-mesenchymal transition (EMT) of the ventral half-somite, the remaining somitic epithelium beneath the surface ectoderm is called the dermomyotome (Christ and Ordahl 1995; Scaal and Christ 2004; Fig. 12.5). The dermomyotomal fate is determined by dorsalizing signals from adjacent structures. These signals are Wnts secreted by the dorsal neural tube and the surface ectoderm. Within the dermomyotome, medial and lateral cells are differently specified. The formation of the medial dermomyotome depends on Wnt1 and Wnt3a from the neural tube (Spence *et al.* 1996; Dietrich *et al.* 1997; Fan *et al.* 1997; Marcelle *et al.* 1997; Capdevila *et al.* 1998; Ikeya and Takada 1998; Wagner *et al.* 2000), whereas the lateral dermomyotome requires Wnt6 from the surface ectoderm (Fan *et al.* 1994; Dietrich *et al.* 1997; Schmidt *et al.* 2004). In mice lacking both dorsomedial signals Wnt1 and Wnt3a, the medial domain of the dermomyotome is lacking, whereas the lateral domain, marked by *Sim1*, is extended medially (Ikeya and Takada 1998). Molecular markers of the dermomyotome include *Pax3* and *Pax7* (reviewed by Stockdale *et al.* 2000). *Pax3*, which is first expressed in the cranial part of the segmental plate, continues to be expressed globally in the newly formed epithelial somites. It is subsequently down-regulated in the ventral half of the somite and the somitocoele cells, ultimately becoming restricted to the dorsomedial and ventrolateral lips of the dermomyotome (Fig. 12.20).

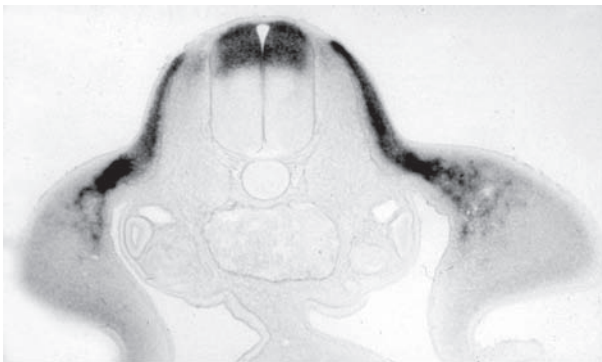


Fig. 12.20 Transverse section of a 3-day embryo showing *Pax3* expression in the dorsal neural tube, in the dermomyotome, and in myogenic cells invading the limbs. Original.

12.7.3 Muscle Formation

All skeletal muscles of the vertebrate body originate from the dermomyotome with the exception of head muscles. Muscle is the phylogenetically oldest derivative of the somite (reviewed in Brand-Saberi and Christ 2000). Still in recent fishes, the myotome represents the largest and earliest formed somitic domain (reviewed in Brennan *et al.* 2002). In the avian embryo, the muscle

compartment can be experimentally enlarged by an increase of Wnt signaling (Wagner *et al.* 2000).

12.7.3.1 Initiation of myogenesis

The paraxial mesoderm is specified to form muscle by influences from adjacent tissues. It has been shown by ablation experiments in the avian embryo that the neural tube, the surface ectoderm, and the notochord-floor plate complex are involved in the induction of myogenesis (Christ *et al.* 1992; Rong *et al.* 1992; Bormann and Yorde 1994; Buffinger and Stockdale 1994; Stern and Hauschka 1995; Cossu *et al.* 1996). A balanced signaling of both Sonic hedgehog (Shh) from the notochord-floor plate complex (Fig. 12.21A) and Wnts from the dorsal neural tube and surface ectoderm acts to initiate myogenesis. The first molecular manifestation of muscle differentiation is the expression of MRFs (muscle regulatory factors). In the avian embryo, the first known MRF to be expressed is *MyoD* (Fig. 12.21B) followed by *Myf5*. Mice lacking both of these MRFs lack all skeletal muscles. *Pax3* is a key regulator of myogenesis and is suggested to activate the putative myogenesis inducer Wnt5b (Linker *et al.* 2003). Myogenesis is negatively regulated by BMPs (Pourquié *et al.* 1996). Thus, the onset of myogenesis in the medial part of the

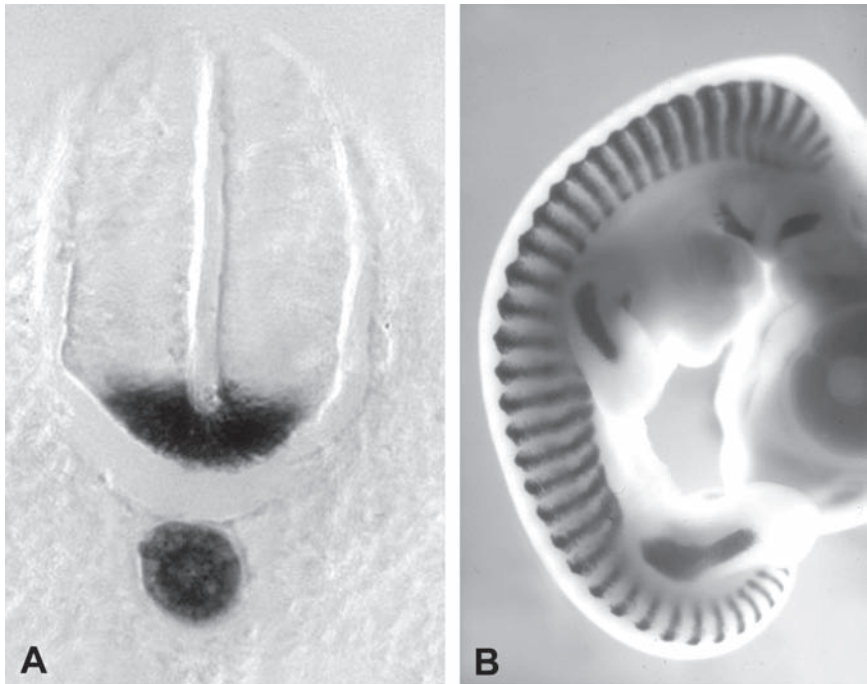


Fig. 12.21 **A.** Transverse section of a 2-day embryo with *Shh* expression in the notochord and floor plate of the neural tube. **B.** *MyoD* expression in the myotomes, the limbs, and the tongue anlage of a 5-day embryo. Original.

dermomyotome is accompanied by the synthesis of the BMP-antagonist Noggin in the dorsomedial somite (Reshef *et al.* 1998).

12.7.3.2 Epaxial myogenesis

A third cellular layer, the myotome, becomes visible between the sclerotome and the dermomyotome at its medial-most edge called the dorsomedial lip (DML; reviewed in Christ and Ordahl 1995; Scaal and Christ 2004; Fig. 12.5). All myotomal cells originate from the dermomyotome (Christ *et al.* 1978). The primitive myocytes become craniocaudally elongated and soon span the craniocaudal extent of the somitic segment. This process requires localized deepithelialization of cells from the dermomyotome and their subsequent translocation into the myotomal domain.

The mechanisms of myotomal cell recruitment have been studied in detail during the last decade (Denetclaw *et al.* 1997, 2001; Kahane *et al.* 1998, 2001, 2002). Gros *et al.* (2004) have demonstrated by *in vivo* electroporation that in a first step, myotomal cells are only provided by the dorsomedial lip (DML) of the dermomyotome by direct ingression and bidirectional extension. In a second step, the caudal and cranial dermomyotomal borders also start to release epaxial myotomal precursor cells. In the epaxial domain, the myotome gives rise to the intrinsic back muscles (Ordahl and Le Douarin 1992).

12.7.3.3 Hypaxial myogenesis

Within the hypaxial domain of the dermomyotome, musculature develops in two fundamentally different modes depending on the axial level of the somites. At cervical and trunk levels, the lateral dermomyotome edge forms a lip, the ventrolateral lip (VLL), from which the formation of the hypaxial myotome is organized similarly to the situation at the DML in the epaxial domain (Gros *et al.* 2004). The ventral parts of the dermomyotomes and the adjacent myotomes invade the lateral plate mesoderm to form abdominal and intercostal muscles (Christ *et al.* 1983).

At limb level, however, the cells of the lateral dermomyotome do not form a VLL, but deepithelialize and migrate into the limb buds to form muscles (Christ *et al.* 1974, 1977; Fig. 12.32). Deepithelialization of muscle precursor cells from the dermomyotome is induced by Scatter factor/HGF (Brand-Saberi *et al.* 1996; Scaal *et al.* 1999) that is being secreted by lateral plate mesodermal cells at the basis of the limb anlagen. Mice deficient for SF/HGF or its receptor *c-met* that is activated in the hypaxial dermomyotome, lack limb muscles because their precursor cells do not delaminate from the dermomyotome (Bladt *et al.* 1995; Schmidt *et al.* 1995). The same phenotype is seen in mutants lacking *Pax3* which is essential for *c-met* transcription (Epstein *et al.* 1996; Tajbakhsh *et al.* 1997). Similar to the situation at limb level, in the hypaxial domain of the occipito-cervical somites 2-6, a population of migratory cells detach from the lateral dermomyotomes and migrate into the tongue rudiment to form muscle (Schemainda 1981; Huang *et al.* 1999, 2001).

Late steps of muscle differentiation up to the formation of multinucleated myotubes depend on multiple factors including Myogenin, Mef2, and MRF4 (reviewed in Buckingham *et al.* 2003).

12.7.4 Dermis

The dermis, which is also known as corium, is a layer of connective tissue between the epidermis and the underlying subcutis. In the 19th century, embryologists realized that the skin is of dual developmental origin, the dermis deriving from the mesoderm as opposed to the ectoderm-derived epidermis. Remak (1850) and Koelliker (1879) concluded that the whole dermis derives from the somatopleure. In 1875, Goette challenged this view by suggesting that the dermis mesenchyme arises from the dermatome, the dorsal compartment of the somite.

The first experimental approach to clarify these conflicting assumptions was undertaken by Murray (1928a,b). He grafted pieces of the lateral plate mesoderm together with overlying ectoderm on host chorioallantoic membranes and found that the lateral and ventral dermis are indeed formed by the somatopleure, thus re-establishing the hypothesis by Remak and colleagues. Experimental evidence of dermis origin was achieved using the quail-chick marking technique that was introduced by Le Douarin (1969, 1973). It has been shown that the dermis of the back is somite-derived (Fig. 12.36) while the dermis of the ventrolateral body wall originates from the somatopleure (Mauger 1972; Christ *et al.* 1983). In addition, quail-chick chimerization identified cranial neural crest cells as precursors of the dermis of the head and partly of the neck (Le Lièvre and Le Douarin 1975).

Regarding the origin of the back dermis, the question was as to the existence of a specific dermogenic compartment in the somite. Olivera-Martinez *et al.* (2000) came to the conclusion that dermis forms only from the medial half of the somite. The subcutis underlying the dermis, which is also of somitic origin, was found to behave likewise. These results have recently been challenged by Ben-Yair *et al.* (2003) by suggesting that the entire mediolateral extent of the somite contributes to the formation of back dermis. By clonal analysis of the central part of the dermomyotome, it has been shown that single dermomyotome cells give rise to both dermis and muscle during the conversion of the dermomyotome epithelium into mesenchyme, suggesting that this dorsal somite derivative must be composed of at least bipotent progenitors (Ben-Yair and Kalcheim 2005).

12.8 INTERMEDIATE MESODERM

The paraxial mesoderm and the lateral plate mesoderm are separated by a non-segmented strip of mesodermal cells, the intermediate mesoderm (Figs. 12.13, 12.15). It consists initially of two layers of cells, dorsal and ventral. The dorsal layer is continuous with the dorsal wall of the segmental plate or somites, and the somatic layer of the lateral plate mesoderm. The ventral layer

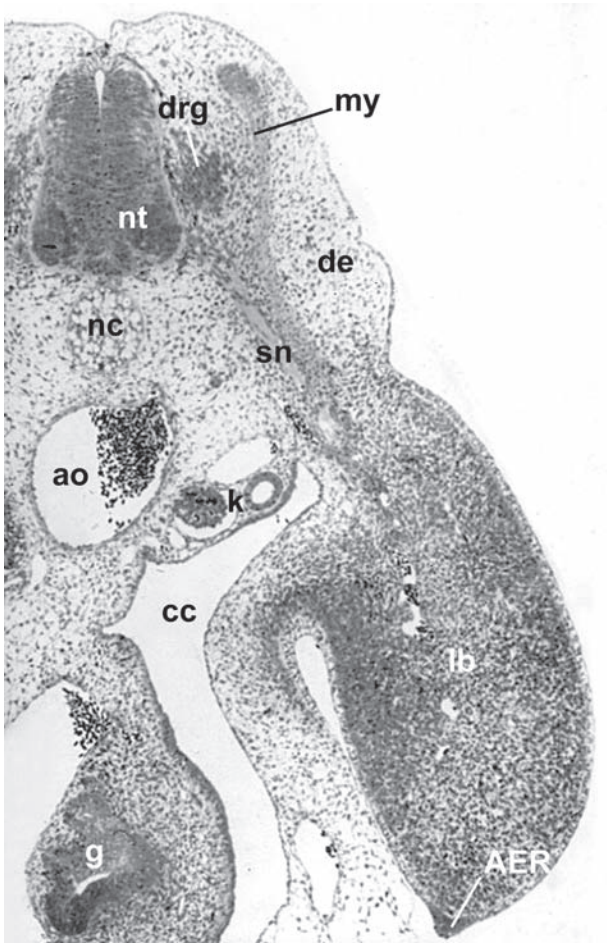


Fig. 12.22 Transverse section of a 4-day embryo. Aorta (ao), neural tube (nt), notochord (nc), gut (g), dorsal root ganglion (drg), myotome (my), spinal nerve (sn), kidney (k), coelomic cavity (cc), limb bud (lb), apical ectodermal ridge (AER). Original.

is continuous with the ventral wall of the segmental plate or somites and the splanchnic layer of the lateral plate mesoderm. In its cervical part, the intermediate mesoderm gives rise to a dorsally situated, segment-overbridging, initially mesenchymal ridge that is the anlage of the pronephric duct, which subsequently becomes epithelialized and canalized (Jacob *et al.* 1978, 1984, 1987). It continuously grows caudally, remaining mesenchymal at its tip until it reaches the cloaca. The tip cells have long cell processes which make contacts with adjacent tissues and are required for orientation and the caudal elongation of the duct, which, at the thoracic level, is called Wolffian duct (Figs. 12.13, 12.15).

12.8.1 Kidney

The kidney of amniotes develops in three generations, from cranial to caudal there is the pronephros, the mesonephros and the metanephros. The main structure of the pronephros is the pronephric duct that gives rise to both the Wolffian duct of the mesonephros (Figs. 12.13, 12.15), and the ureter of the metanephros. Kidney development is characterized by reciprocal inductive interactions between the duct epithelium and the intermediate mesoderm-derived mesenchyme, the nephrogenic mesoderm. This is true for both the mesonephros and the metanephros. The caudal part of the common nephric duct, the ureter bud, gives rise to the ureter, the Pelvis renalis and, by extensive branching, to the collecting ducts. The basic structural unit of the kidney is the nephron which originates from the nephrogenic mesoderm by a mesenchymal-to-epithelial transition. The first step in kidney differentiation is the formation of mesenchymal aggregates close to the duct epithelium. The mesenchymal cells turn on *Pax2* expression. From these aggregates, comma- and, subsequently, S-shaped epithelial bodies develop under the control of Wnt-4 (Stark *et al.* 1994) and elongate to tubules (Fig. 12.23). An important signal from the mesenchyme was identified as glial-derived neurotrophic factor (GDNF) whose receptor Ret is expressed in the ureteric bud. The competence of the mesenchyme to become induced depends on the expression of the zink-finger transcription factor WT1. FGF2 secreted by the ureteric bud

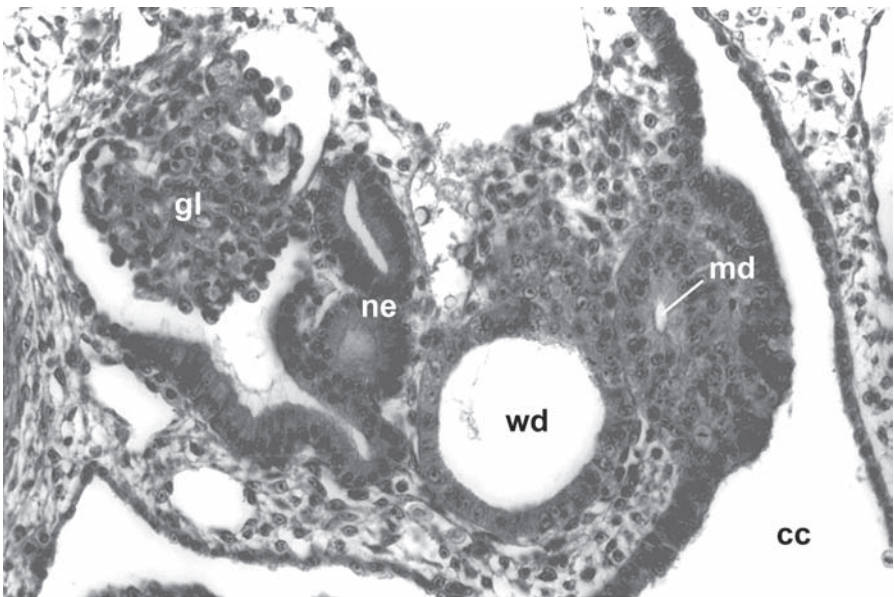


Fig. 12.23 Transverse section of a 6-day embryo. Coelomic cavity (cc), Wolffian duct (wd), Müllerian duct (md), nephric tubules (ne), glomerulus (gl). Original.

is suggested to maintain survival of the mesenchyme and to induce *Pax2* expression. The leukemia inhibitory factor (LIF) is involved in the induction of tubulus formation (Bard *et al.* 1996; Lechner and Dressler 1997; Barasch *et al.* 1999). *Pax2* and *Lim-1* are being expressed in both the epithelium of the duct and in the tubules (Barnes *et al.* 1994; Warady *et al.* 1994; Keller *et al.* 1994; Torres *et al.* 1995). The correct development of the nephrons depends on polycystin 1 and 2 (Ward *et al.* 1996; van Adelsberg 1997).

12.8.2 Gonadal Development

The first stages of gonadal development do not depend on the presence of germ cells. The main genital structures such as the gonads, sexual ducts and external genitalia pass through a morphologically indifferent stage in which they cannot be identified as being either male or female. Later, they become determined to develop in a fashion that is characteristic of the respective sex. Without specific feminizing influences, such as the hormone estrogen, they develop into a male type. Whether the gonad forms an ovary or testis depends on the chromosome constitution; ZW for females and ZZ for males. The *DMRT1* gene on the Z chromosome is a candidate masculinizing factor, while *ASW/HINTW* on the W chromosome is a candidate feminizing factor (see Chapter 13). From their earliest appearance the gonads are intimately associated with the nephric system. The gonads arise as ridge-like thickenings (gonadal ridges) in the ventromedial face of the mesonephros consisting of a mesenchymal core covered by the mesothelium, the epithelial lining of the coelomic cavity.

The primordial germ cells are early separated from the somatic cells and can be identified by their large size, high alkaline phosphatase activity, or germ cell-specific monoclonal antibodies in the anterior germinal crescent located beyond the future head region of primitive streak embryos (Eyal-Giladi *et al.* 1981; Hahnel and Eddy 1986). They pass through the walls of local blood vessels and enter circulation where they are being transported by the blood stream, from which they penetrate the wall of the gonadal blood vessels to settle down in the gonads of 3-day chick embryos. The genital ridge epithelium proliferates into the loose connective mesenchymal tissue forming the sex cords which later on give rise to testis cords in the male and the follicle cells in the female. Gonadal sex differentiation is described in more detail in Chapter 13.

The Müllerian (paramesonephric) duct (Fig. 12.23) develops in close vicinity to the Wolffian duct and originates from the epithelial lining of the coelomic cavity by invagination of the mesothelium. The part thus formed is relatively short; the major portion is added by elongation of the cranial part which grows caudally to reach the cloaca on the seventh day. The growth of the Müllerian duct occurs in close proximity to the Wolffian duct. They share a common basement membrane. In the male, the Müllerian duct becomes rudimentary and disappears under the influence of the Müllerian inhibiting factor, a glycoprotein secreted by the Sertoli cells of the testis; in the female, it

becomes the oviduct on the left side and degenerates on the right side. The Wolffian duct persists in the male and functions as the vas deferens transporting sperm to the cloaca.

12.9 LATERAL PLATE MESODERM

The lateral plate mesoderm consists of two layers, the somatic mesoderm, and the splanchnic mesoderm with the coelomic cavity in between (Figs. 12.5, 12.13). The somatic mesoderm borders on the surface ectoderm with which it interacts during further development (e.g. limb development). The splanchnic mesoderm develops in interactions with the adjacent endoderm. Laterally, the lateral plate mesoderm is continuous with extraembryonic tissue. The terminology for the lateral plate mesoderm is somewhat confusing. In some textbooks (e.g. Lillie's *Development of the Chick*, Patten's *Foundations of Embryology* ed. by B.M. Carlson) the term *somatopleure* is used for the somatic mesoderm plus surface ectoderm and the term *splanchnopleure* for splanchnic mesoderm plus endoderm. In other text books and original papers, the terms *somatopleure* and *splanchnopleure* are used only for the mesodermal layers proper. We here follow the usage which terms the mesodermal layers plus ectoderm or endoderm, *somatopleure* and *splanchnopleure*, respectively. The mesodermal layers alone are called somatic (parietal) and splanchnic (visceral) mesoderm.

12.9.1 Somatopleure

The somatopleure (Figs. 12.5, 12.13) forms the ventrolateral body wall. Its outer epithelial layer is the ectoderm that differentiates into epidermis. Its inner layer, the mesothelium, represents the lining of the body cavity, the coelom. The somatic mesoderm located in between forms the dermis and the connective tissue of the thoracic and abdominal wall and gives rise to tendons and the sternum (Fell 1939; Chevallier *et al.* 1975, 1977; Christ *et al.* 1983) whereas the ribs and muscles originate from the somites. The sternum begins to form at day 8 as a bilateral pair of mesenchymal condensations. These sternal plates migrate ventrally and eventually fuse together in the midline. The most conspicuous derivatives of the somatopleure are the limbs.

12.9.1.1 Limbs

The amphibians, reptiles, birds and mammals belong to the tetrapods as they have four limbs, a pair of forelimbs known as legs, arms or wings, and a pair of hindlimbs. The limbs develop from the somatopleure as a result of interactions between somatic mesoderm and ectoderm (Figs. 12.7A, 12.22). The somatic mesoderm gives rise to the skeleton, the dermis, the connective tissue, and to smooth muscle of the limb, whereas the epidermis arises from the ectoderm. Skeletal muscle develops from muscle precursor cells that originate from the somites and invade the limb buds.

The bulk of experimental work to analyze the processes of limb development has been done in the chick embryo and has been supplemented

by data from mouse knockouts. The early specification of the limb fields is likely to be controlled by the axial *Hox* code that leads to an expression of FGF10 initially in the paraxial mesoderm and subsequently in the prospective limb bud itself. Knock-out studies with mouse embryos have shown that FGF10 is necessary and sufficient to specify the somatic mesoderm and to induce limb development (Ohuchi *et al.* 1997). The formation of limb buds is a consequence of different proliferation activities of the somatic mesoderm at limb bud levels and in between (Hornbruch and Wolpert 1970). The fore- and hindlimb can be distinguished by the different expression of T-box genes, with *Tbx5* expressed in the forelimb bud and *Tbx4* in the hindlimb bud. The T-box genes are required for the initiation of limb outgrowth. Limb identity is controlled by the *Hox* code and for the hindlimb by *Pitx1* (Minguillon *et al.* 2005). Further limb morphogenesis is characterized by an elongation of the bud which is brought about by an intense proliferation of cells in the distal-most part of the limb bud mesoderm, the progress zone. This is the labile region of the limb bud within which the new proximal-distal levels of the appositionally growing limb bud are being laid down (Summerbell 1974). An early event in chick limb bud development is the formation of the apical ectodermal ridge (AER) that is induced by FGF10. The AER (Figs. 12.22, 12.24A) demarcates dorsal from ventral epidermis. The dorsal ectoderm expresses *Wnt7a*, the ventral ectoderm expresses *engrailed-1*. These genes establish the dorsal and ventral identity of the limb (Riddle *et al.* 1995; Vogel *et al.* 1995; Chen *et al.* 1998; Loomis *et al.* 1996). If the AER is removed, a FGF4 bead can substitute for it and bring about continued growth and proximo-distal patterning (Niswander *et al.* 1993).

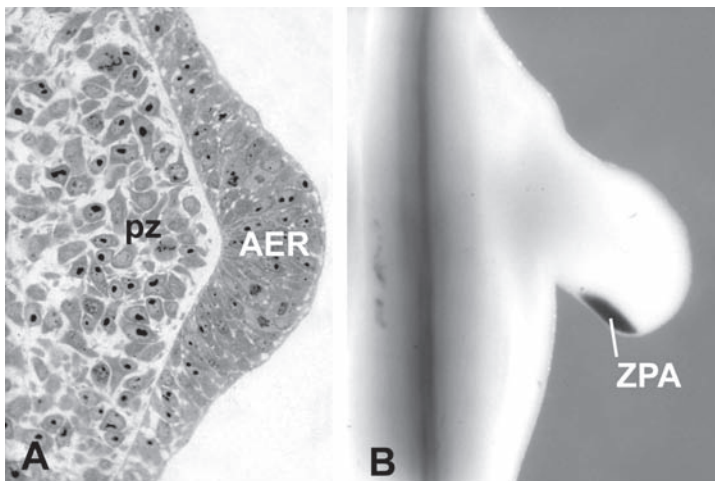


Fig. 12.24 Limbs of a 4-day embryo. **A.** Section through the tip. Apical ectodermal ridge (AER), progress zone of the limb mesoderm (pz). **B.** Dorsal view showing the expression of *Shh* in the zone of polarizing activity (ZPA). Original.

The function of the AER as a signaling center needs a factor from the mesoderm, which is called the AER maintenance factor. This maintenance activity is partly accounted for by Sonic hedgehog (Shh) from the posterior part of the limb bud mesoderm (Niswander *et al.* 1994).

The anteroposterior pattern of the limb is controlled by a mesodermal area at the posterior margin of the bud, the zone of polarizing activity (ZPA; Fig. 12.24B; Tickle *et al.* 1975). After transplantation of a second ZPA to the anterior margin of the limb, a second set of distal structures is induced in a mirror symmetrical arrangement to the original set. The signal produced by the ZPA that is responsible for anteroposterior polarity could be identified as Sonic hedgehog (Shh; Riddle *et al.* 1993). The ZPA creates a Shh gradient with the highest concentration posteriorly and the lowest concentration anteriorly which can be interpreted by the mesodermal cells of the limb bud to form a skeletal pattern (Gritli-Linde *et al.* 2001; Zeng *et al.* 2001). Limb patterning is additionally controlled by *Hox* genes. *Hoxd* and *Hoxa* genes are serially expressed from posterior to anterior (*Hoxd9* to -13) and from proximal to distal (*Hoxa9* to -13). It is suggested that the expression pattern of *Hox* genes is partly controlled by signaling molecules like Shh and that the *Hox* genes encode states of determination for different parts of the limb.

12.9.1.2 Splanchnopleure

The splanchnopleure consists of the splanchnic (visceral) mesoderm and the adjacent endoderm (Figs. 12.5, 12.13). It forms the gut and gives rise to the circulatory system including the heart, blood cells and blood vessels. The circulatory system is the first organ system to function in the developing embryo (Fig. 12.27).

12.9.1.3 Heart

The heart arises from two regions of the splanchnic mesoderm. The precursors of heart muscle have been identified in the anterior part of the primitive streak behind Hensen's node (Garcia-Martinez and Schoenwolf 1993; Lopez-Sanchez *et al.* 2001). CITED2, a member of the CITED family of transcription factors is the earliest marker of these cells known to date (Schlange *et al.* 2000). It is suggested that the endoderm plays an important role in the specification and migration of the myocardial precursor cells. In the course of gastrulation, these mesodermal cells migrate in an anterolateral direction to form the cardiogenic mesoderm (Garcia-Martinez and Schoenwolf 1993). The migration of the heart precursors from the primitive streak is controlled by the transcription factors *Mesp1* and *Mesp2* (Kitayima *et al.* 2000). In 18 to 20 hours chick embryos the prospective heart cells move anteriorly between the ectoderm and endoderm towards the midline of the embryo, remaining in close contact with the endoderm (Linask and Lash 1986). Another population of cells that contribute to the formation of the heart comes from the pharyngeal splanchnic mesoderm. These cells form the secondary (anterior) heart field which contributes to the formation of the right ventricle and the outflow tract (reviewed in Brand 2003).

The endoderm adjacent to the heart fields is responsible for the induction of cells to become committed to the myocardial fate (Alsan and Schultheiss 2002). Cerberus, BMP2 and activin induce the expression of the transcription factor Nkx2.5 in the migrating heart precursor cells (Komuro and Izumo 1993; Lints *et al.* 1993; Sugi and Lough 1994; Schultheiss *et al.* 1995; Andree *et al.* 1998). Nkx2.5 activates the synthesis of other transcription factors of the GATA and MEF families that instruct the mesoderm to become cardiac muscle by inducing the expression of genes encoding cardiac muscle-specific proteins.

After mesoderm specification of the heart fields and during formation of the foregut by inward folding of the splanchnic mesoderm, the paired heart anlagen come together and fuse in the midline to form a single tube. If this process of fusion is impaired the two heart tubes can persist (Cardia bifida; Gräper 1907; DeHaan 1959). Mutant mice with an inactivation of GATA5 and HAND2 or disturbed endoderm development, show a Cardia bifida (Molkentin *et al.* 1997; Roebroek *et al.* 1998; Saga *et al.* 1999; Reiter *et al.* 1999; Alexander *et al.* 1999). It is suggested that regionalization of the heart tube is controlled by *Hox* genes.

Further heart morphogenesis (looping) is characterized by an increasing left-right-asymmetry (Fig. 12.25). As mentioned in the section on gastrulation, *nodal* expression in the left splanchnic mesoderm induces *Pitx2*, that is activated in the left atrium, the ventral part of the ventricle and the outflow tract (Campione *et al.* 2001). The function of *Pitx2* could be to enhance cell proliferation via activation of Cyclin-D2 expression and in this way to control heart morphogenesis.

Looping begins at HH-stage 10 and normally occurs to the right side of the embryo. The right ventricular wall bulges outwards and becomes convex while the left wall becomes concave. At the same time, the heart rotates to the right (Fig. 12.25). An important role in the control of normal looping is played by *BMP4*, *HAND1*, *HAND2* and *Tbx 20* (reviewed in Brand 2003). During the process of looping, the separation of the atrial part from the ventricle part becomes conspicuous (Fig. 12.25) and can be visualized by the expression of the transcription factors *Hey1* and *Hey2* (Leimeister *et al.* 1999; Nakagawa *et al.* 1999). Ventricular heart muscle expresses the homeobox protein *Irx4*, whereas atrial muscle is characterized by the expression of *GATA5* and the T-box gene *Tbx5*. *HAND1* and *HAND2* are required for the development of the ventricles. *HAND1* is expressed in the myocardium of the left ventricle and *HAND2* in that of the right ventricle (Thomas *et al.* 1998). Recent studies have shown that endocardial and epicardial derived-FGF signals are involved in myocardial proliferation and differentiation (Lavine *et al.* 2005). The proliferation of endocardial cells is controlled by VEGF and plays an important role in the trabeculation of the ventricle walls (Feucht *et al.* 1997).

The epicardium, which is the outer layer of the vertebrate heart in contact with the fluid of the pericardial cavity derives from a primarily extracardiac primordium, the proepicardial serosa. From there, the epicardial cells spread

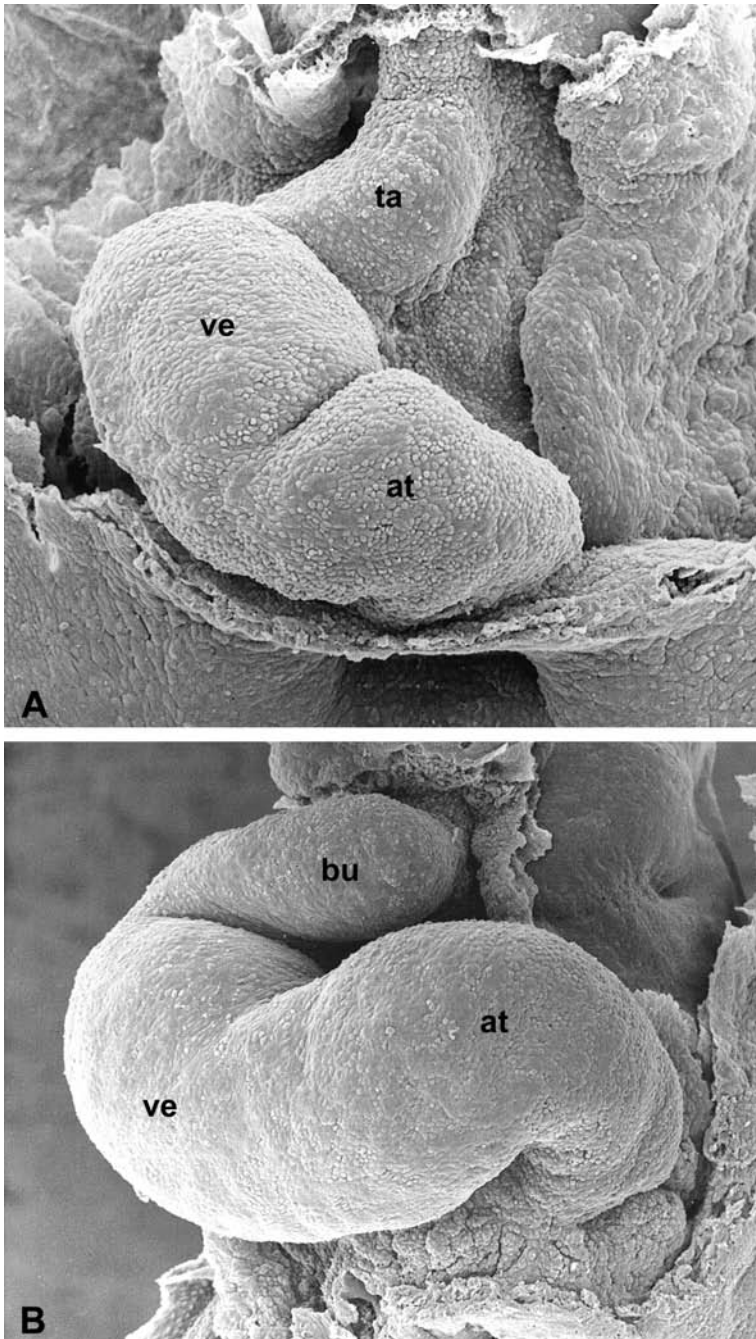


Fig. 12.25 Scanning electron micrographs of the developing heart. **A.** HH-stage 12 embryo. **B.** HH-stage 14 embryo. Atrium (at), ventricle (ve), bulbus (bu). Truncus arteriosus (ta). Courtesy of Dr. J. Männer, Göttingen.

as a continuous epithelial sheet over the naked myocardial surface and provides nearly all cellular elements of the subepicardial and intermyocardial connective tissue, and of the coronary vasculature (reviewed in Männer *et al.* 2001).

12.9.1.4 Blood vessel formation

Blood vessel formation is intimately connected to the early development of blood cells. It is suggested that endothelial cells and blood cells share a common precursor, the hemangioblast. Both cell types have some common marker proteins on the cell surface (Wood *et al.* 1997; Choi *et al.* 1998; Liao and Zon 1999). Two different modes of blood vessel formation can be distinguished: vasculogenesis and angiogenesis (Risau 1995, 1997; Risau and Flamme 1995). Vasculogenesis describes the *de novo* formation of vascular tubes from *in situ* differentiating endothelial cells. This process can only be observed in the early embryo. Later on, blood vessels only emerge from already differentiated endothelial cells of older vessels by remodeling.

Vasculogenesis begins in the wall of the yolk sac (reviewed in Wilting *et al.* 2003). The first sign of endothelial cell formation is the appearance of mesodermal clusters, the hemangioblastic aggregates.

The aggregates mature into blood islands, the external cells of which are flatter and differentiate into endothelial cells, while the internal cells become hematopoietic stem cells (Fig. 12.8). The endothelial cells form tubes and connect to form a network of capillaries, the primary capillary plexus. Blood island formation depends on endoderm-derived signals (Wilt 1965; Pardanaud *et al.* 1989). In this process, FGF2, GATA-4 and Indian hedgehog may act in concert with VEGF (vascular endothelial growth factor) (Flamme and Risau 1992; Bielenska *et al.* 1996; Dyer *et al.* 2001; Damert *et al.* 2002). The mesodermal cells that differentiate into angioblasts express the vascular endothelial growth factor receptor-2 (VEGFR-2) (Eichmann *et al.* 2002, reviewed in Wilting *et al.* 2003). Vasculogenesis also occurs in the embryo proper within the splanchnic mesoderm close to the endoderm (Fig. 12.26A) to form the aorta and major veins (Yancopoulos *et al.* 2000). This is also true for the first steps of coronary vessel formation in the epicardium-derived mesoderm on the surface of the developing heart.

Angiogenesis takes place after an initial phase of vasculogenesis. It is characterized by loosening of cell contacts at certain points of the capillaries, degradation of the extracellular matrix and migration as well as proliferation of the endothelium-derived angioblasts, a process that is known as sprouting (Carmeliet 2000; Fig. 12.26B). As vessels differentiate, they become successively invaded by mesenchymal (periendothelial) cells that give rise to pericytes, smooth muscle cells, and fibrocytes. Angiopoietin-1 (Ang1) and PDGF are involved in the recruitment and differentiation of periendothelial cells.

There is complementary expression of *ephrin-B2* in arterial endothelial cells, and *Eph-B4*, its cognate receptor, in venous endothelial cells, from early developmental stages until adulthood (Adams *et al.* 1999). Venous endothelial

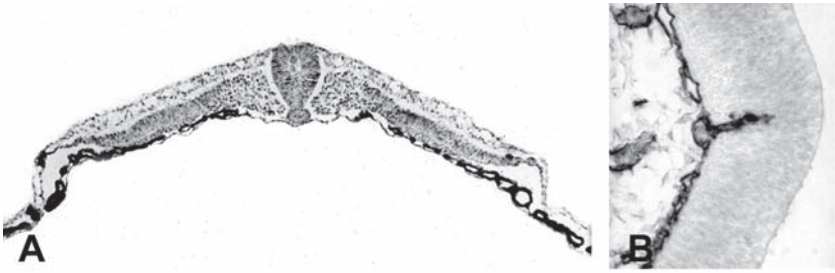


Fig. 12.26 Development of blood vessels in quail embryos. The vessels are stained with an antibody specific for quail endothelial cells (QH1). **A.** HH-stage 10 embryo. Blood vessels formed in the splanchnic mesoderm close to the endoderm by vasculogenesis. **B.** Sprouting of a blood vessel from the perineural vascular plexus into the neuroepithelium illustrating angiogenesis. Original.

cells express arterial markers when integrated in arteries, showing a considerable plasticity of endothelial cells (Moyon *et al.* 2001; Othman-Hassan *et al.* 2001).

12.9.1.5 Lymphangiogenesis

The formation of lymphatic vessels (Fig. 12.7B), lymphangiogenesis, starts much later than that of blood vessels (3 to 4 days later in the chick). The first anlagen of the lymphatics are the jugular, posterior and retroperitoneal lymph plexus, which develop either by sprouting from venous endothelium or by *in situ* differentiation from mesenchymal cells, or by both mechanisms (reviewed in Wilting *et al.* 2001). The early lymphatic plexus are then remodelled into lymph sacs by fusion of vessels. Markers of lymphatic endothelial cells include *VEGFR-3* and *Prox1* (reviewed in Wilting *et al.* 2003). Lymphatic and blood vessel endothelial cells do not only derive from the splanchnic mesoderm but also from the paraxial mesoderm (Wilting *et al.* 1995, 2000, 2001; Schneider *et al.* 1999).

12.10 ENDODERM

The endoderm develops in close association with the adjacent splanchnic mesoderm and takes the early lead in determining the fundamental organization of the digestive and respiratory tract. Later, the mesoderm generates the signals that specify the regional characteristics of gut and gland morphogenesis as well as endodermal cell differentiation.

12.10.1 Gut

The gut develops from the splanchnopleure and is characterized by an inner epithelial layer that originates from the endoderm (Figs. 12.5, 12.28), and the tissues of the wall that are derivatives of the splanchnic mesoderm. The gut additionally gives rise to the respiratory tube and lungs, liver, gallbladder,

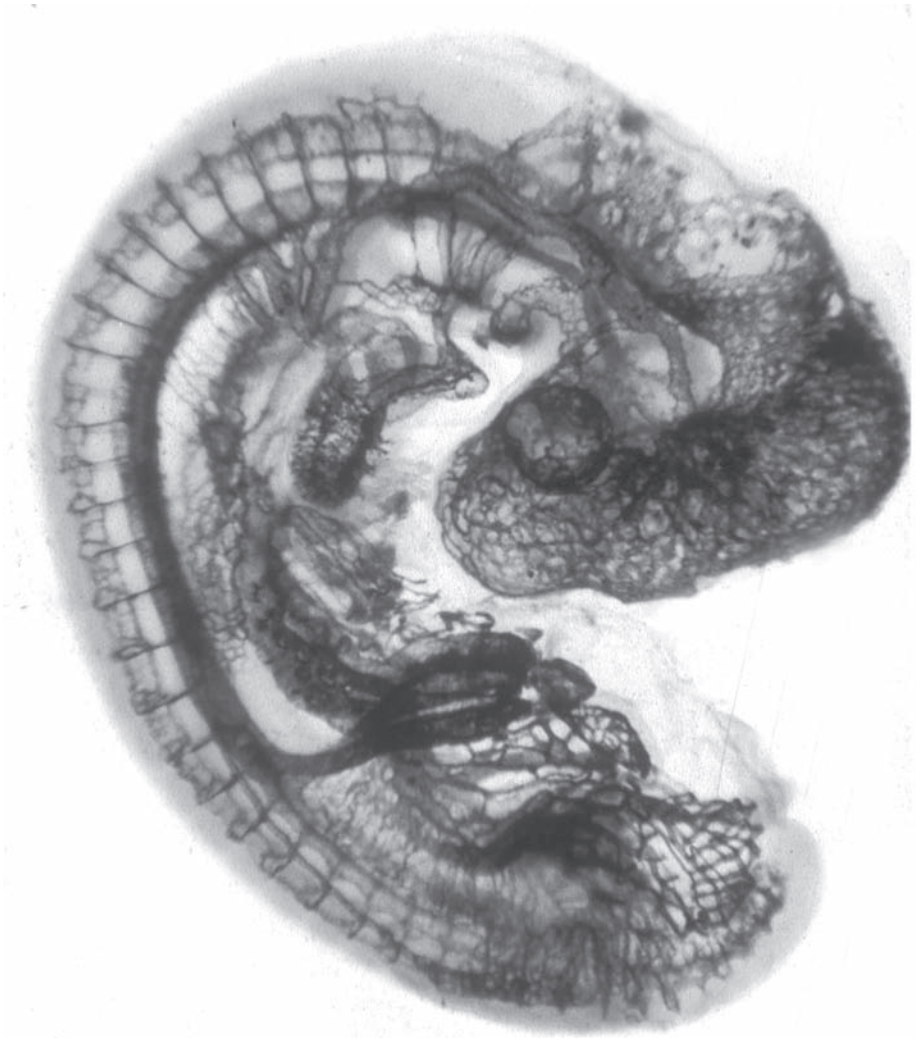


Fig. 12.27 4-day embryo. The vascular system is visualized by Indian ink injection. Original.

pancreas, and the allantois which contributes to the chorioallantoic membrane that acts as a gas exchange organ of the avian embryo (Freeman and Vince 1974; Paganelli 1991) and has the additional function to absorb calcium ions from the shell.

The gut of birds shows species-specific characteristics. The food passes directly through the esophagus and collects at a diverticulum at its lower end, the crop. From here, it enters the cranial part of the stomach, the proventriculus. It then passes into a highly muscular part of the stomach, the gizzard. At its caudal end, the gut is not separated from the urinary and genital ducts,

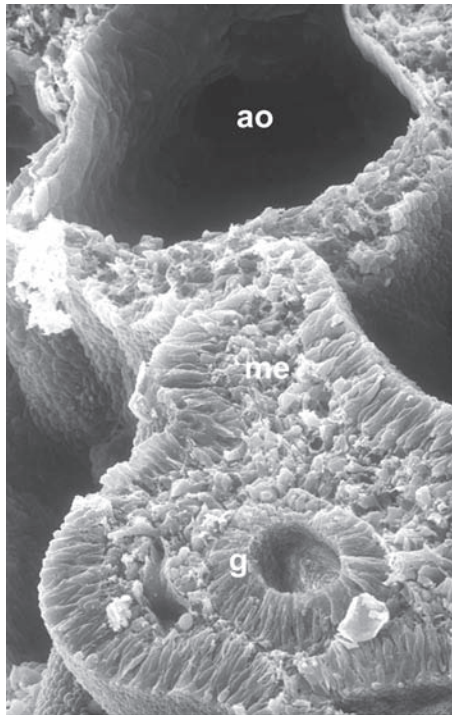


Fig. 12.28 Scanning electron micrograph of the gut of a 4-day embryo after transverse fraction. Aorta (ao), mesentery (me), endodermal gut tube (g). Original.

sharing with them a common cloaca which is transitorily closed by the cloacal membrane where the gut endoderm meets the surface ectoderm.

The primitive gut is formed by the folding of the body and the fusion of the splanchnopleural folds and consists of the foregut, midgut and hindgut. The first part is cranially located, ending blindly at the stomodeal plate. It is surrounded by head mesenchyme, which is more caudally replaced by splanchnic mesoderm. The hindgut forms similar to the foregut due to the caudally directed growth of the embryo and gives rise to the gut caudal to the caeca. The midgut transitorily lacks a ventral wall and is in communication with the yolk sac. It is represented by the small intestine, beginning at the liver and reaching to the caeca, of which birds have two. The foregut gives rise to the pharynx, esophagus, stomach and the small intestine down to the liver.

The specification of the gut tissue is a result of interactions between endoderm and splanchnic mesoderm. It is suggested that Shh secreted by the endoderm is involved in this process (Roberts *et al.* 1995; 1998). It is secreted in different concentrations at different sites. Its receptor, Patched, is expressed in the splanchnic mesoderm and activates a set of *Hox* genes in the mesoderm that probably specify different gut regions (Yokouchi *et al.* 1995; Roberts *et al.* 1998).

The most cranial part of the foregut is the pharynx. Here, the avian embryo produces four pairs of well-developed pharyngeal pouches and a fifth one that is smaller (Fig. 12.29). These pouches coincide on the outside with ectodermal grooves. Between the pouches and grooves are the pharyngeal arches. The first pair of pharyngeal pouches gives rise to the tubo-tympanic recessus; the second to fourth ones to the thymus and parathyroids and the fifth one to the ultimo-branchial bodies (Le Douarin *et al.* 1984; Kameda 1984, 1993). The derivatives of the pharyngeal arches are cartilage and muscle. Each arch is served by an aortic arch artery. The muscle precursor cells in the arches come from the paraxial head mesoderm; the fibroblasts and chondrocytes from the neural crest.

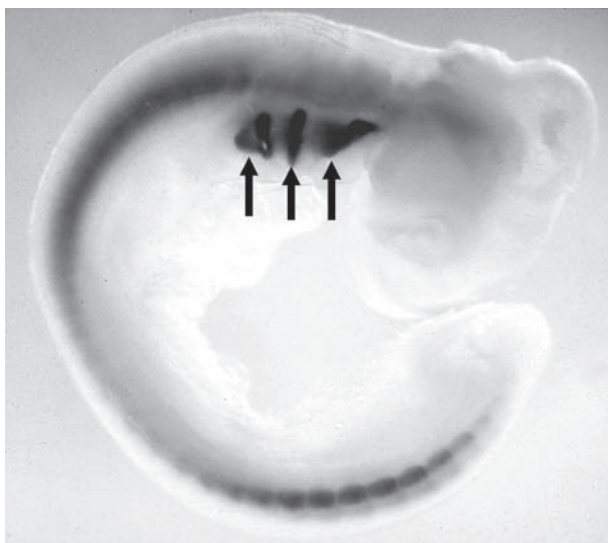


Fig. 12.29 3-day embryo. The pharyngeal pouches are visualized by *Pax9* expression (arrows). Original.

12.10.2 Liver

The early specification of liver-forming cells is a result of interactions between the endoderm of the foregut caudal to the stomach and the cardiogenic mesoderm. The developing heart appears to block an inhibitor of liver-specific gene transcription by FGFs (Jung *et al.* 1999). First signs of this specification are the induction of serum albumin- and α -fetoprotein-mRNA in the endoderm cells. These cells proliferate under the influence of the adjacent splanchnic mesoderm and form the hepatic diverticulum that subsequently branches into two diverticula; an anterior and posterior one, which are later separately open into the duodenum. Following the branching processes, the diverticula form the glandular epithelium of the liver (Dunwoodie *et al.* 1998). The early liver-specific transcription factors include Hepatocyte Nuclear Factor-3 β (HNF-3 β) and GATA4 (Weinstein *et al.* 1994; Molkenstein *et al.* 1997). The liver rudiment

forms hepatic cords with mesenchymal cells in between, rapidly grows in size, and becomes invaded by blood-forming stem cells (Fig. 12.30). Mouse mutants with inactivated genes for *c-jun*, *Hlx*, *GHF/SF* and *c-met* die because of insufficient liver development (reviewed in Duncan 2003).

12.10.3 Pancreas

The pancreas consists of an exocrine and endocrine glandular tissue and develops in birds from three rudiments, a dorsal one and two ventral ones, which start to fuse together at day 6. In the adult domestic fowl, three

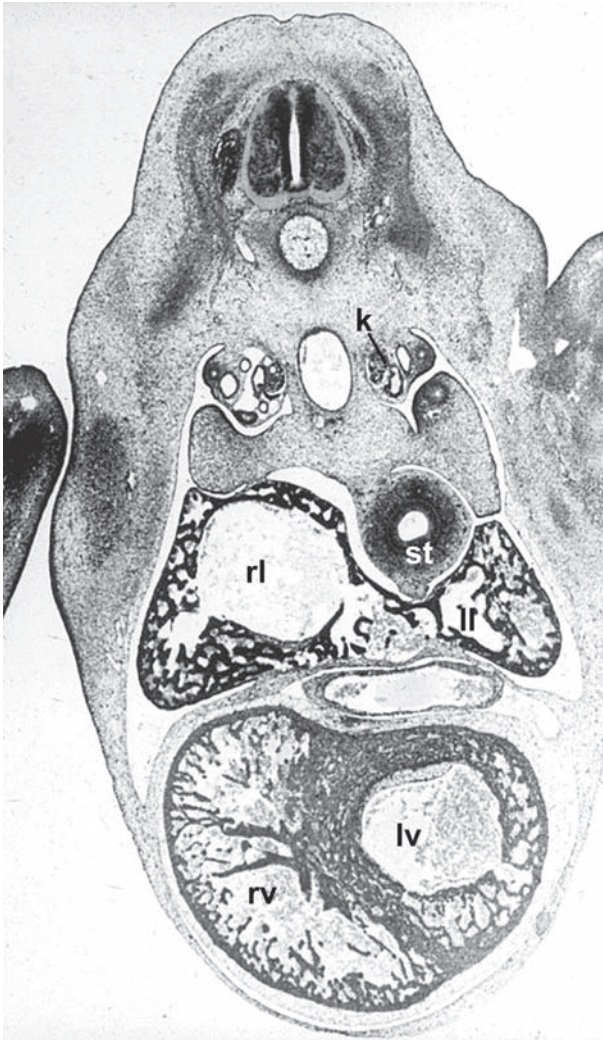


Fig. 12.30 Transverse section of a 6-day embryo at thoracic level. Right lobe of liver (rl), left lobe of liver (ll), proventriculus of stomach (st), kidney (k), right ventricle (rv), left ventricle (lv). Original.

pancreatic ducts are present that open near the end of the duodenum in close vicinity of the two bile ducts. In contrast to liver formation, where the cardiac mesoderm blocks liver inhibiting influences of the notochord, pancreas formation is actively promoted by the notochordal signals. The notochordal factors FGF2 and ActivinB activate pancreas formation by repressing *Sonic hedgehog* expression in the gut endoderm (Apelqvist *et al.* 1997; Hebrok *et al.* 1998). As a result, the pancreatic endoderm expresses the transcription factors PDX1 and IPF1 (Insulin Promoting Factor 1) which are required for pancreas formation (Johnson *et al.* 1994; Ahlgren *et al.* 1996; Offield *et al.* 1996). Precursors of the islet cells become separated from the distal duct epithelia.

The decision on exocrine or endocrine fate of pancreatic cells is controlled by follistatin, a BMP inhibitor, that is secreted by the mesenchyme. It promotes the commitment to exocrine cell fate (Miralles *et al.* 1998). Cell diversification within the islets is controlled by *Pax* genes. Initially, the islet cells express *Pax6* and *Pax4*. Those cells that retain both *Pax6* and *Pax4* become insulin-producing β -cells, whereas the cells that down-regulate *Pax4* differentiate into glucagon-producing α -cells (Sosa-Pineda *et al.* 1997; St-Onge *et al.* 1997).

12.10.4 Respiratory System

The respiratory tract of birds consists of the larynx cranialis, trachea, larynx caudalis (syrinx), bronchi and lungs (Fig. 12.31). In addition, birds develop air sacs that occupy many bones. The first sign of its development is the laryngo-tracheal groove at the floor of the pharynx posterior to the fourth pair of pharyngeal pouches. From there the bronchial tree starts to arise during day 3 with its proximal trunk, the trachea. First, the groove bifurcates into two main branches that form the paired lungs. Since the larynx, trachea, bronchi and lungs are derivatives of the gut, they are lined by an endodermal epithelium which is surrounded by mesoderm that gives rise to smooth muscle, connective tissue, and blood vessels. The bronchial budding is controlled by the adjacent mesoderm. Numerous tissue recombination experiments have shown that the mesoderm surrounding the trachea inhibits budding whereas the mesoderm surrounding the bronchial buds promotes budding. Epidermal growth factor (EGF) and TGF- β are associated with the growth and budding of lung buds (Alescio and Cassini 1962; Lawson 1983; Heine *et al.* 1990). Lung development also requires an interplay between FGFs and Shh.

12.11 COELOM AND MESENTERIES

The coelom or body cavity develops within the lateral plate mesoderm (Fig. 12.9), separating the upper somatic layer beneath the ectoderm from the lower, splanchnic layer associated with the endoderm. In the early embryo the coelomic cavities of both sides are separated by the axial and paraxial structures. Laterally, each coelomic cavity extends to the extraembryonic region. With the formation of the head fold, the paired coelomic cavities extend anteriorly to form the amnio-cardiac vesicles which unite anterior to

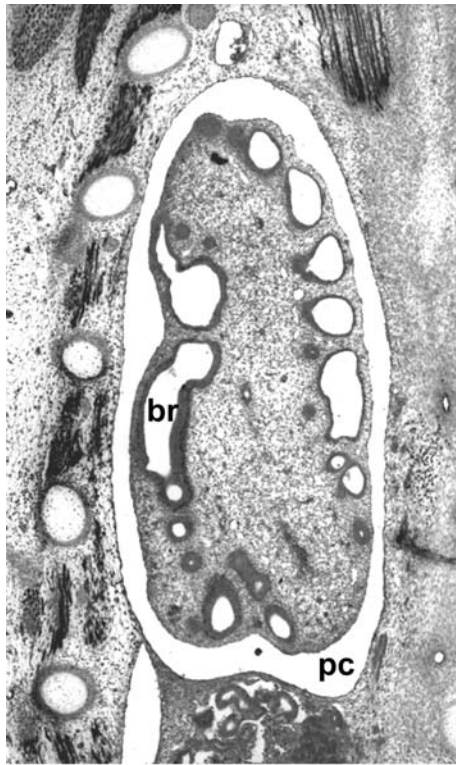


Fig. 12.31 Sagittal section through a lung of a 8-day embryo. Bronchus (br), pleural cavity (pc). Original.

the head. The lateral regions subsequently join to form the heart, whereas the more anterior part, the proamnion, gives rise to the amnion. During formation of the foregut by an infolding of the splanchnopleure and somatopleure (lateral body folds) the left and right coeloms come closely together only separated by the fused splanchnic mesoderm of both sides that forms a dorsal and ventral mesentery (Fig. 12.49). As the ventral mesentery survives only at liver level, more caudally both coelomic cavities come into communication. The coelomic cavity becomes subdivided in three parts, the pericardial, pleural and peritoneal cavities.

12.12 ECTODERM

The ectoderm (Figs. 12.13, 12.14) gives rise to the epidermis, the nervous system and the organs of special sense. The nervous system includes the central and peripheral nervous system; and the central nervous system can be subdivided into the brain and the spinal cord which both are derivatives of the neural tube (see section 12.6, Neurulation).

12.12.1 Central Nervous System

During and following induction, the neural primordium becomes subdivided into four main parts, the forebrain, midbrain, hindbrain, and spinal cord (Fig. 12.32A). The first step in craniocaudal patterning of the nervous system is the specification of forebrain identity. Since cranial markers like *Otx2* are already expressed in the avian epiblast prior to neural induction, it appears that regionalization of the neural primordium is a very early event during avian development (Bally-Cuif *et al.* 1995; Niss and Leutz 1998; Shamim and Mason 1998). It has been shown that the cranial identity is induced by signals from node-derived mesendodermal cells that underlie the cranial neural plate (Knoetgen *et al.* 1999).

There is increasing evidence that the inhibition of BMP and Wnt signaling is involved in head induction (Glinka *et al.* 1997, 1998). It seems that the more caudally located epiblast cells that are initially also fated to form forebrain structures, become respecified to form midbrain and hindbrain by caudalizing factors secreted by the paraxial mesoderm such as FGFs and retinoic acid which induce *Hox* genes (Muhr *et al.* 1999; Cox and Hemmati-Brinvanhou 1995; Lamb and Harland 1995).

The forebrain then becomes subdivided into the telencephalon and diencephalon (Fig. 12.32), which both become further regionalized to form specific domains. The craniocaudal patterning of the midbrain is regulated by an organizing center located at the isthmus between the midbrain and hindbrain vesicles, the isthmus organizer (Fig. 12.32B), whose cells produce FGF8 and control the regional specification of the neural tissue on both the midbrain and cranial hindbrain side by interacting with other genes such as *Pax1*; *En1*, *Wnt1* (Crossley *et al.* 1996; Seikh and Mason 1996; Martinez *et al.* 1999). The hindbrain meets cranially the midbrain and caudally the spinal cord. In contrast to other regions of the central nervous system, the hindbrain is overtly segmented and consists of eight units, the rhombomeres numbered 1 to 8 from cranial to caudal. The first rhombomere gives rise to the cerebellum. Each subsequent pair of rhombomeres is the source of one cranial nerve: The trigeminal nerve (V) originates from rhombomeres 2 and 3, the facial nerve (VII) from rhombomeres 4 and 5 and the glossopharyngeal nerve (IX) from rhombomeres 6 and 7. Rhombomeres 2,4 and 6 contribute neural crest cells to the branchial arches. The rhombomeres represent developmental compartments having specific identities (Guthrie and Lumsden 1991). The clonal restriction of rhombomeres is initiated and maintained by the expression of ephrins and Eph receptors in alternating rhombomeres (Xu *et al.* 1995; Xu and Wilkinson 1997).

In contrast to the brain, the spinal cord does not show a morphologically overt craniocaudal pattern. Its rudiment, the caudal and longest part of the neural tube, however, is molecularly patterned in craniocaudal direction by boundaries of *Hox* genes, the axial *Hox*-code (Kessel and Gruss 1990). It has been shown that the paraxial mesoderm is involved in the control of craniocaudal patterning of the spinal cord (Ensini *et al.* 1998).

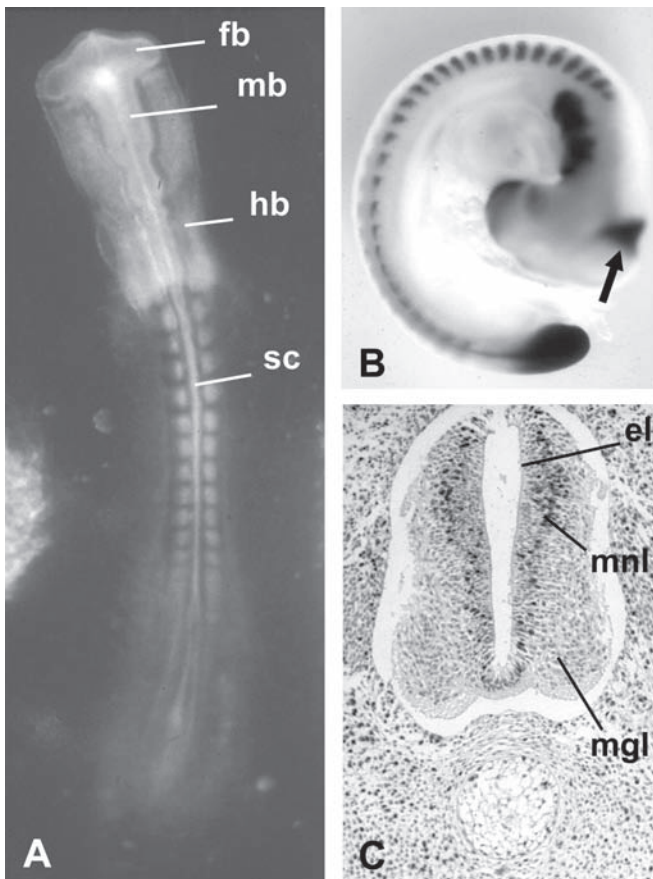


Fig. 12.32 Development of the central nervous system. **A.** HH-stage 11 embryo. Forebrain (fb), midbrain (mb), hindbrain (hb), anlage of the spinal cord (sc). **B.** 3-day embryo showing *FGF8* expression. Isthmus (arrow) between midbrain and hindbrain vesicles. **C.** Transverse section through a 6-day embryo. S-phase nuclei are stained. Ependymal layer (el), mantle layer (mnl), marginal layer (mgl). Original.

Like the brain, the spinal cord is dorsoventrally patterned (van Straaten *et al.* 1985, 1988; Placzek and Furley 1996; Tanabe and Jessell 1996). This patterning is mediated by ventralizing signals emanated from both the notochord (Fig. 12.21A) as well as the somites and, on the other hand, dorsalizing signals produced by the surface ectoderm. One molecule with ventralizing influence has been identified as Sonic hedgehog that initially represses the expression of various transcription factors in the ventral neural tube such as *Pax3* (Fig. 12.20) and *Pax7* (Jessell 2000). Another ventralizing factor is somite-secreted retinoic acid (Diez del Corral *et al.* 2003; Novitsch *et al.* 2003; Pierani *et al.* 1999; Wilson *et al.* 2004). Later, the floor plate itself takes over the signaling role of the notochord by producing Shh. The surface ectoderm expresses *BMP4* and *BMP7*, both having dorsalizing influences. This

function is being continued by the roof plate of the neural tube which secretes dorsalin in addition to BMPs (Basler *et al.* 1993). This dorsoventral polarization of the developing spinal cord is the prerequisite for the origin of ventrally located motor neurons and dorsally located sensory and commissural neurons.

The neural tube of a 2.5-day chick embryo processes two layers, the ventricular (ependymal) layer which lines the neural canal and contains a large number of mitotic cells, and the outer layer which is called the marginal layer and gives rise to the white matter. Postmitotic neuroblasts which leave the inner ventricular layer form an intermediate layer of densely packed cells, called the mantle layer, from which the gray matter arises (Fig. 12.32C).

12.12.2 Peripheral Nervous System

Each spinal nerve has both a somatic and splanchnic component as well as both motor and sensory components. The motor neurons located in the ventral horn of the spinal cord send out axons that form the ventral roots (Fig. 12.33). The cell bodies of sensory neurons are located in the dorsal root ganglia which are derivatives of the neural crest (Figs. 12.18, 12.22, 12.33). These neurons send processes into the spinal cord forming the dorsal roots and processes into the periphery that contact the skin or other specialized sensory structures. As a consequence of the restriction of emigrating neural crest cells

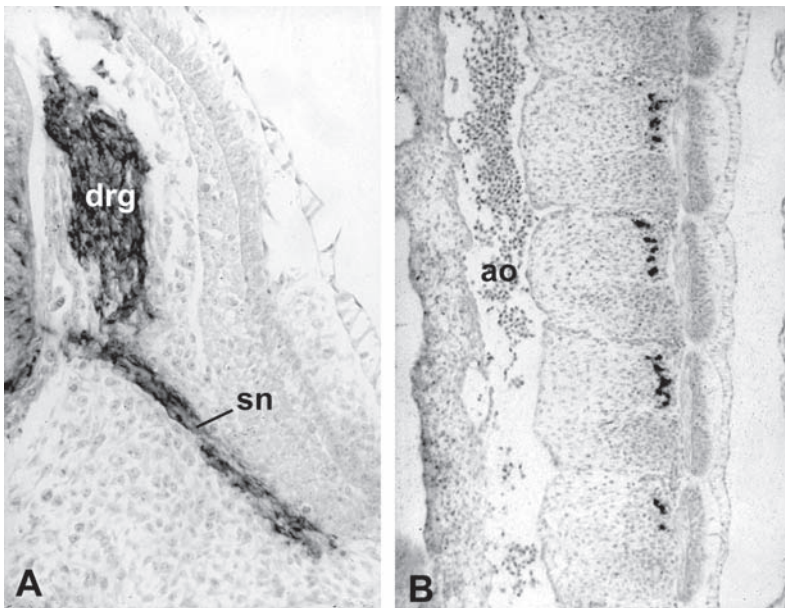


Fig. 12.33 Development of the peripheral nervous system. 4-day embryos stained with HNK-1 antibody. **A.** Transverse section. Dorsal root ganglion (drg), spinal nerve (sn). **B.** Oblique section. Axons invading the cranial half of the sclerotomes. Aorta (ao). Original.

and axons to the cranial half of the sclerotomes, the peripheral nervous system becomes segmented (Keynes and Stern 1984; Rickmann *et al.* 1985; Fig. 12.33B). The outgrowing axons explore the environment by specialized structures located at their tips, the growth cones, which send out pseudopodial projections. These filopodia retract from unfavorable substrates and remain fixed to favorable ones directing the entire nerve process into a certain direction.

A variety of environmental influences is involved in the process of axonal guidance (Tosney 1991; Keynes *et al.* 1997). Growth cones interact with both stationary cells and extracellular matrix. As the outgrowing neurite approaches its target, it may be attracted to it by a short-range gradient of growth factors or neurotrophic substances.

The autonomic nervous system is of neural crest origin. All the sympathetic ganglia arise from the neural crest posterior to the level of the fifth somite. From levels of somites 18th to 24th the adreno-medullary cells originate. The enteric nervous system is formed by neural crest cells from somite levels 1-7, the so-called vagal crest, with the exception of the ganglion of Remak and the enteric nervous system of the gut posterior to the yolk stalk which both receive neural crest cells from sacral levels caudal of the 28th somite (Le Douarin 1986). The neural crest cells migrate on two pathways: a dorsolateral and a ventral one. Both pathways are separated by the dermomyotome. The cells that migrate along the dorsolateral pathway differentiate into pigment cells. The ventral pathway branches into two different routes. One branch from this common pathway leads into the cranial halves of the sclerotomes. Cells that take this pathway aggregate within the sclerotomes to form dorsal root ganglia. The second branch of this pathway is directed ventrally and cells on this pathway form major components of the sympathetic nervous system and the adrenal medulla. It has been shown that these cells become progressively committed by influences of the environment through which they migrate. BMP2 and BMP4 secreted by the aorta, for instance, induce autonomic neurons to become committed to an adrenergic fate (Varley and Maxwell 1996; Reissmann *et al.* 1996). Unlike trunk neural crest cells, the cranial neural crest cells contribute additionally to connective tissue, dermis, and skeletal elements of the head (Couly *et al.* 1993). The cranial neural crest cells appear to be imprinted with morphogenetic instructions that relate to their level of origin (Noden 1983).

12.12.3 Organs of Special Sense

12.12.3.1 Eye

An optic vesicle develops on either side of the prosencephalon. It approaches the head ectoderm. The vesicle becomes invaginated and forms the optic cup with a proximal layer, the future pigment layer, and a distal layer, the future retina. During this process, the original lumen disappears and a new lumen, the future vitreous chamber, arises (Fig. 12.34A). The invagination of the optic cup does not start at the extreme lateral border of the optic vesicle, but from a

rather more ventral position. This leads to a gap in the continuity of the wall of the optic cup which is known as the choroid fissure. The choroid fissure partially envelops the hyaloid artery which becomes the central artery of the retina and is invaded by axons of nerve cells which differentiate in the retina and form the optic nerve. The lens is formed from the lens placode, an ectodermal thickening, which arises in response to inductive signals from the underlying optic cup. The ectoderm of the lens placode invaginates and forms the lens vesicle (Fig. 12.34A) which sinks beneath the surface ectoderm, the latter becoming the cornea.

Lens induction is mediated by BMP4 produced by cells of the optic vesicle (Furuta and Hogan, 1998). In response to this signaling, the ectoderm expresses *Sox2* and *Sox3*. The ability of the ectoderm to respond to the inductive signal depends on the expression of *Pax6* (Li *et al.* 1994; Fujiwara *et al.* 1994).

12.12.3.2 Ear

The inner ear develops from the otic (auditory) placode, an area of thickened surface ectoderm, as a response to inductive signals from the notochord, paraxial mesoderm and rhombencephalon. The auditory placode is invaginated to form the auditory pit. After closing off from the surface ectoderm the anlage of the ear constitutes a pouch called the auditory vesicle, or otocyst. In

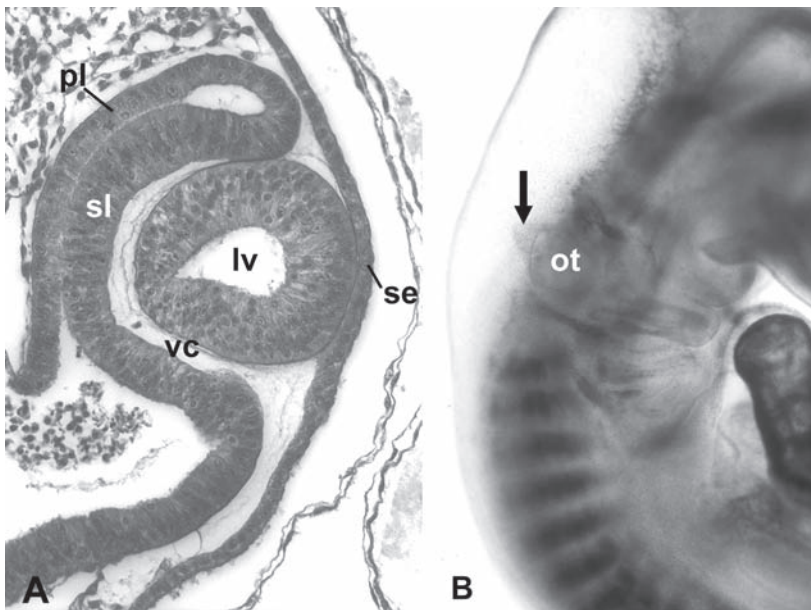


Fig. 12.34 Organs of special sense. **A.** Section through the eye of a 3-day embryo. Lens vesicle (lv), Optic cup consisting of the inner sensory layer (sl, retina) and the outer pigmented layer (pl), surface ectoderm (se, cornea), vitreous chamber (vc). **B.** Head-neck transitional zone of a 4-day embryo. Otocyst (ot), endolymphatic duct anlage (arrow). Original.

the chick embryo, the auditory placodes can be seen at HH-stage 10 on either side of the head just cranial to the first somite. Thus, it is the otocyst that separates the head paraxial mesoderm from the somites (Fig. 12.34B). The dorsal wall of the auditory vesicle grows out to form the blind-ended endolymphatic duct which thus enlarges and forms the endolymphatic sac. The endolymphatic sac undergoes a complex morphogenesis to form the semicircular canals and utricle. Its inferior part gives rise to the sacculus and cochlea.

The middle and outer ear are formed from the first pharyngeal pouch and groove, respectively. The auditory ossicle, the columella, is present as a cartilaginous anlage by day 6 and located between the cochlea and the tympanic membrane, the latter being the wall between the external auditory meatus formed from the first pharyngeal groove and the tympanic cavity formed from the first pharyngeal pouch.

12.12.4 Surface Ectoderm

During neurulation, the surface ectoderm separates from the neuroectoderm to cover the entire outer surface of the embryonic body (Figs. 12.13, 12.14). Being originally a single-layered epithelium, the ectodermal cells start to segregate into two layers as early as HH-stage 5, forming an outer peridermal layer, and an inner basal layer of the prospective epidermis. The periderm persists until approximately 18 days of development (HH-stage 44) when it is sloughed off to expose the definitive epidermis (Sengel 1976). From HH-stage 18, mesenchymal cells populate the space underneath the ectoderm to form a subectodermal mesenchyme, the prospective dermis. These mesenchymal cells originate dorsally from the dermomyotome, ventrolaterally from the somatopleure, and in the head from the neural crest (Mauger, 1972; Le Lievre and Le Douarin, 1975; Christ *et al.* 1983). The further development of all ectodermal derivatives, including skin, feathers, scales, beak, nails, and salivary and lacrimal glands, depends on a complex reciprocal signaling crosstalk between the ectodermal epithelium and the underlying mesenchyme (reviewed in Pispa and Thesleff 2003).

In the skin, development of the epidermis proper and the dermis begins first in the feather-forming regions, the pterylae. Next to the pterylae, there are featherless regions (apteria, Fig. 12.35) where the skin differentiates much later. Starting at HH-stage 26, mesenchymal cell density in the pterylae increases (Wessels 1965) concomitant with the onset of *cDermo-1* expression, which is a marker of feather forming dermis (Scaal *et al.* 2001, 2002; Hornik *et al.* 2005). Upon a yet unknown signal from the mesenchyme, which is likely correlated to cell density (Jiang *et al.* 1999), local ectodermal thickenings appear in hexagonal arrays, which presage the localization of the prospective feather anlagen. These ectodermal placodes signal back to the underlying mesenchyme and induce placode-associated dermal condensations, thus launching an ongoing epithelial-mesenchymal crosstalk leading to feather formation (reviewed in Dhouailly 1977, Yu *et al.* 2004). Several molecules expressed in the dermal condensations, including the bHLH transcription

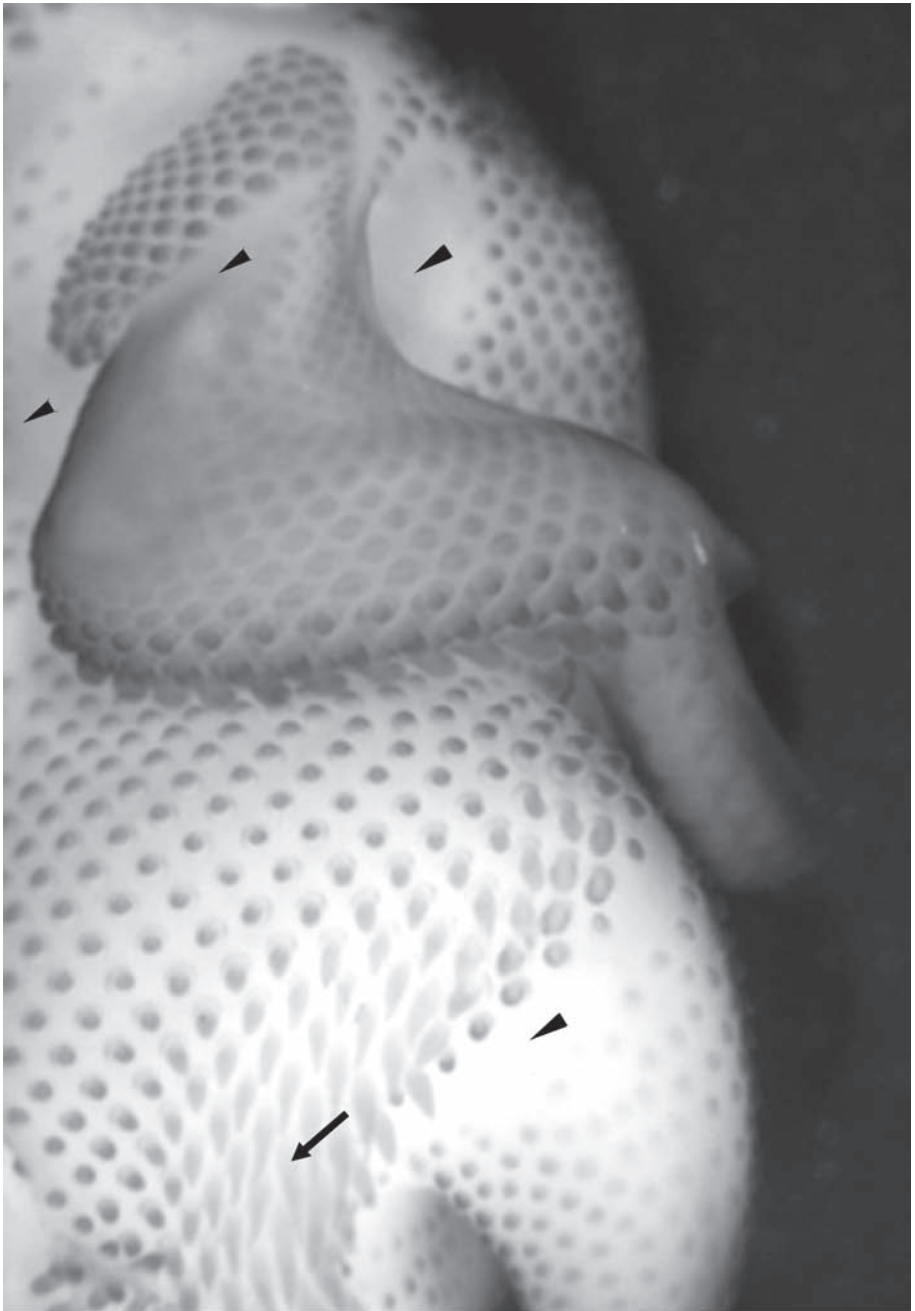


Fig. 12.35 10-day embryo. The feather buds and outgrowing feather filaments (arrow) are visualized by *cDermo-1* expression. Note the apteric regions between the pterylae (arrowheads). Original.

factor *cDermo-1* (Hornik *et al.* 2005; Scaal *et al.* 2002) and FGF10 (Mandler and Neubüser 2004), are sufficient to induce feather development. Likewise, overexpression or application of molecules expressed in the epidermal placodes have been shown to induce feather formation, including FGF2 and 4 (Song *et al.* 1996, 2004; Widelitz *et al.* 1996), Shh (Ting-Berreth and Chuong 1996, Morgan *et al.* 1998), β -catenin (Noramly *et al.* 1999) and Follistatin (Patel *et al.* 1999). Notch/delta signaling is thought to refine the early placode pattern and create a boundary for the already formed dermal condensation of the feather primordium (Crowe *et al.* 1998; Viallet *et al.* 1998). Together with the underlying dermal condensation, the placode forms a prominent feather bud which subsequently elongates to form a thread-like feather filament (Fig. 12.35). The filament finally develops into the mesenchymal and epithelial layers giving rise to the rachis and barbs of the definite feather (Sengel 1976, Yu *et al.* 2004). This process is not well understood, but recent experiments revealed that inhibition of BMP activity promotes rachis and barb branching, whereas overexpression of BMP results in repression of Shh and in increased rachis formation and fusion of barbs (Harris *et al.* 2002; Yu *et al.* 2002). In contrast to the feathered pterylae, the skin of the tarsometatarsus and toes develops scales, which are homologous to feathers and develop similarly (Sengel *et al.* 1976). Tissue recombination experiments have shown that while the initiation and thus localization of an epidermal appendage depends on the dermis, the specific quality, i.e. scale or feather, depends on the competence of the epidermis (Dhouailly 1977). The molecular basis of this is still obscure, but might be due to local differences in dosage of signaling molecules, as overexpression of β -catenin has been shown to be able to convert scales into feathers (Widelitz *et al.* 2000).

Other ectodermal organs seem to be regulated in a similar way to the feathers, which are the best studied example of ectodermal morphogenesis. For instance, the beak develops from a proliferative zone in the frontonasal mass of the chicken embryo (Schneider and Helms 2003). This mesenchyme expresses BMP2 and 4, and is covered by ectoderm expressing FGF8 and Shh (Hu *et al.* 2003). Growth and final size of the beak depends on mesenchymal BMP signaling (Wu *et al.* 2004).

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Molecular Genetics of Avian Sex Determination and Gonadal Differentiation

Craig A. Smith

13.1 INTRODUCTION

Sex determination is a fundamental aspect of avian biology. Differentiation of the sexes during embryonic development is essential for later reproduction and survival of the species. All birds have genetic sex determination, in which sex is established at fertilisation by the inheritance of sex chromosomes. Most birds have identifiable sex chromosomes (ZZ male; ZW female). This chapter will review our current understanding of sex determination in avians, based primarily on studies in the chicken (*Gallus gallus domesticus*). The chicken has long been used as a model in developmental biology, and is a species of agricultural importance. At present, the molecular mechanism of sex determination in chickens and other birds is not known. However, a draft sequence of the chicken genome has now been reported, providing new genetic data, which will help to elucidate the mechanism of avian sex determination (International Chicken Genome Sequencing Consortium 2004; Schmid *et al.* 2005).

13.2 AVIAN SEX CHROMOSOMES

In birds and other vertebrates with genetic sex determination, the inheritance of sex-determining genes carried on sex chromosomes controls male versus female development. Although inherited at fertilisation, these genes are activated during embryonic life, during which they induce the formation of either testes or ovaries (gonadal sex differentiation, Fig. 13.1). After hatching, the release of sex steroid hormones from the gonads then regulates secondary

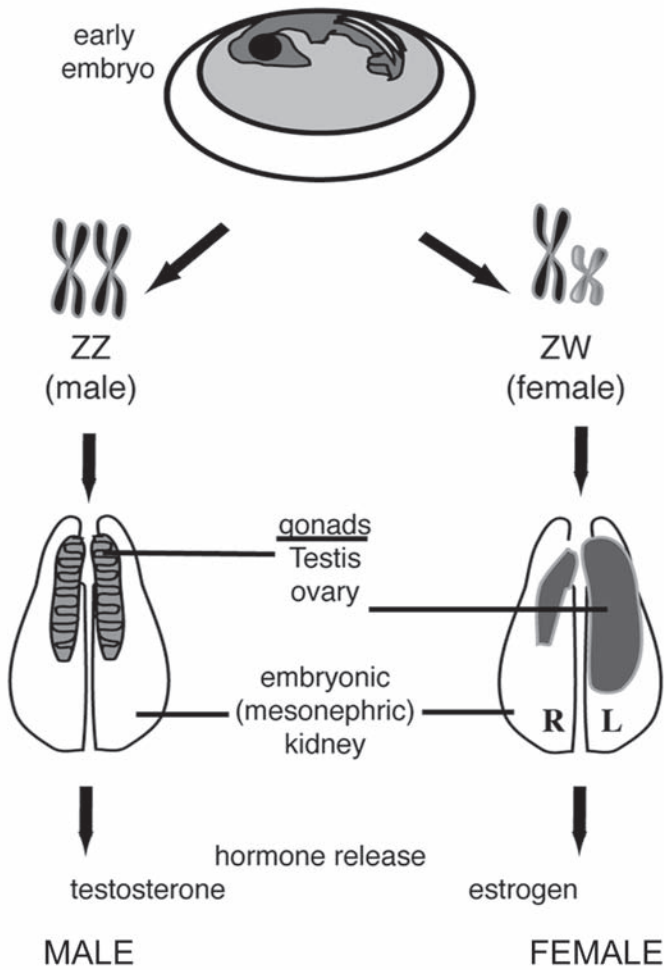


Fig. 13.1 Sex determination and gonadal sex differentiation in birds. Embryos with a ZZ sex chromosome constitution develop bilateral testes, while those with a ZW genotype usually develop a left ovary and right rudimentary gonad. The release of sex steroid hormones from the gonads (testosterone in males and estrogen in females) regulates secondary sexual characteristics.

sexually dimorphic traits, such as behaviour, plumage, wattles and combs (Fig. 13.1). Sex determination therefore ultimately depends upon the sex chromosomes. Most birds have heteromorphic sex chromosomes, that is, sex chromosomes that are morphologically different. These are the large Z and smaller W sex chromosomes. Embryos carrying two Z chromosomes (ZZ) are destined to become males, while those carrying a Z and W (ZW) become

females. In birds, therefore, the female is the heterogametic sex (producing two different types of gametes, some carrying a Z and some carrying a W sex chromosome), while the male is homogametic (all gametes carry the same sex chromosome, Z). This is opposite to the pattern in mammals, in which the male, XY is heterogametic. Interestingly, sex chromosomes are not heteromorphic in the flightless ratites (emus, ostriches, rheas and their relatives). In these birds, the sex chromosomes are virtually indistinguishable, as assessed by chromosomal morphology (Ansari *et al.* 1988; Ogawa *et al.* 1998). This could reflect the ancestral state in birds, because ratites (Palaeognathae) are considered to be oldest avian lineage (Paton *et al.* 2002; van Tuinen *et al.* 2000). Heteromorphic sex chromosomes prevail in all other, more derived, birds (carinates). However, some DNA sequence analyses suggest that passerine (perching) birds are basal to both Galliformes (chickens, quail) and Struthioniformes (ratites) (Härlid and Arnason 1999). If so, then the evolution of heteromorphic sex chromosomes of most modern birds may be relatively recent. However, a basal position for passerines is not supported in the present volume from molecular (Volume 6A, Chapter 1) and spermatological (Volume 6A, Chapter 8) evidence. Although ratites have non-differentiated, virtually homomorphic sex chromosomes, these chromosomes must nevertheless carry a sex determining gene/s.

The large Z sex chromosome represents between 7 and 10% of the avian haploid genome. The Z is well conserved across birds, including ratites (Saitoh *et al.* 1993; Nanda *et al.* 1998; Shetty *et al.* 1999 2002), and it carries a large number of so-called “house-keeping” genes (Fig. 13.2). In this regard, the Z is analogous to the mammalian X chromosome, but it is not homologous, having evolved from a different ancestral autosome (non sex chromosome) (Fridolfsson *et al.* 1998; Graves and Shetty 2001). In fact, the chicken Z chromosome is largely syntenic (having conserved blocks of genes) with human chromosome 9 (Nanda *et al.* 1999). It also has some regions that are equivalent to parts of human chromosome 4, 5 and 8 (Ellegren 2000; Nanda *et al.* 2000; International Chicken Genome Sequencing Consortium 2004). One gene that maps to the Z sex chromosome in all birds examined, including ratites, is *DMRT1* (*Drosophila* Doublesex and *C. elegans* Mab-3 Related Transcription factor, #1). This gene encodes a transcriptional regulation protein and is a potential sex determinant (Fig. 13.2; see section 13.6.1 below).

The avian W sex chromosome is small and mostly heterochromatic in the majority of birds (Fig. 13.2). However, in some raptors and cranes, the W is relatively large, and in ratites it is equivalent in size to the Z (De Boer and Sinoo 1984; Ogawa *et al.* 1998). Studies in Galliformes (chickens, quails, turkeys) show that the small W chromosome is late replicating and it pairs with a small region of the Z during female meiosis (Solari *et al.* 1988). In contrast, in ratites, the large W chromosome pairs with the Z chromosome along most of its length. In the chicken, approximately 80% of the W chromosome comprises repetitive DNA sequences of the *Xho1*, *EcoRI* and *Ssp1* classes (Fig. 13.2) (Kodama *et al.* 1987; Saitoh *et al.* 1991; Saitoh and Mizuno

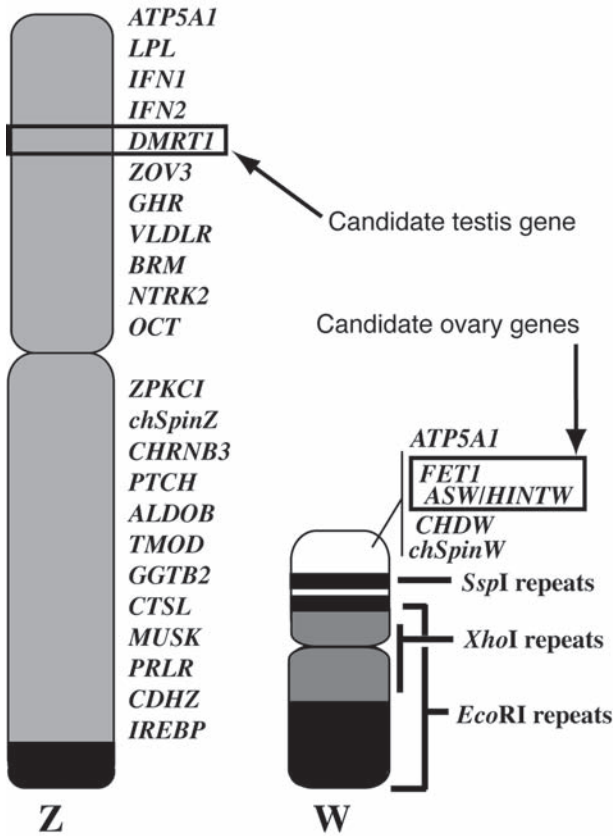


Fig. 13.2 Chicken Z and W sex chromosomes. Euchromatin is shown in light grey, heterochromatin in black. The candidate sex-determining genes, *DMRT1*, and *ASW* and *FET 1*, are boxed. The small W chromosome harbors extensive repeats of the *EcoR1*, *Xho1* and *Ssp1* classes. Exact gene order of mapped genes may vary from that shown. Reproduced with permission from Smith and Sinclair (2004). Bioessays, 26: 120-132, Fig. 24.2.

1992; Suka *et al.* 1993; reviewed in Mizuno *et al.* 2002). Only a few functional genes have been identified on the avian (chicken) W chromosome. Of those that have been well described, many have homologues on the Z chromosome, such as *ATP5A1*, *SPIN* and *CHD* (Fig. 13.2). Using gene density estimates based on the distribution of currently known W-linked genes, Mizuno and his colleagues predicted that between fifteen and 45 genes in total will be found on the W chromosome (Mizuno *et al.* 2002). Indeed, at least forty five known or predicted genes have currently been assigned to the W chromosome, based on the chicken genome sequencing project (http://www.ensembl.org/Gallus_gallus/index.html). It appears that the avian W chromosome, like the mammalian Y chromosome, has undergone degenerative change during

evolution, due to suppression of genetic recombination between the proto-sex chromosomes. In other vertebrates, suppression of recombination between the sex chromosomes is due to the emergence of sexually dimorphic genes (Ohno 1967). In birds, this implies that an ovary-determining gene has been isolated on the W, or a gene has been lost from the W (setting up a Z dosage mechanism of sex determination).

Sex-specific sequences on the female (W) sex chromosome have been used as molecular sexing tools in birds. In the chicken, PCR-amplification of the repetitive W-linked *Xho1* sequence provides a robust method of sexing embryonic and hatchling birds. The sex-linked chromo-helicase DNA binding gene (*CHD*) has also been used to sex non-ratite birds. It has both W- and Z-linked orthologues, which can be discriminated by PCR (Ellegren 1996). Itoh and colleagues reported the presence of a non-repetitive W-linked element, thought to be a pseudogene, in all bird species examined (including ratites). This sequence can be used to sex birds at the molecular level. The sequence has a Z-linked orthologue, which is sufficiently different from the W copy to be distinguishable by PCR in all birds except ratites (Itoh *et al.* 2001).

13.3 Z CHROMOSOME DOSAGE VERSUS THE DOMINANT W HYPOTHESIS

The mechanism of avian sex determination at the molecular level remains unknown. Sex might be determined by the dosage of Z chromosomes (two for males, one for females), by a dominant feminising gene on the W chromosome, or by both mechanisms. In mammals, early studies confirmed that the presence of the Y chromosome dictates testis development, regardless of the number of X chromosomes. This is proven by the phenotype of individuals with sex chromosome aneuploidy. Those with an XXY karyotype (Klinefelters Syndrome) develop as males, while those with an XO karyotype (only one X chromosome, Turner's syndrome) are female. However, similar sex chromosome aneuploids have only rarely been reported in birds, and some may be embryo lethal (Graves 2003). Early reports of apparent ZZW birds, or gynandromorphic birds (male on one side of the body, female on the other side) were not informative because definitive karyotype analysis was not carried out (Crew 1933; reviewed in Thorne 1995). More recently, a gynandromorphic zebra finch (Fig. 13.3) was carefully examined and found to be ZW on the female side of the body, and ZZ on the male side. This bird provided evidence that the sex chromosomes directly contribute to differences in brain sex (the neural song circuit), rather than through gonadal hormones alone, but it was not informative with regard to the Z dosage versus dominant W hypotheses. Arit *et al.* (2004) reported a breeding female Reed warbler (*Acrocephalus arundinaceus*) with an apparent 2A:ZZW genotype, supporting the dominant W hypothesis. However, the bird was identified as ZZW due to the inheritance of Z-linked microsatellite markers and it was not karyotyped, so the presence of a W chromosome was not demonstrated.

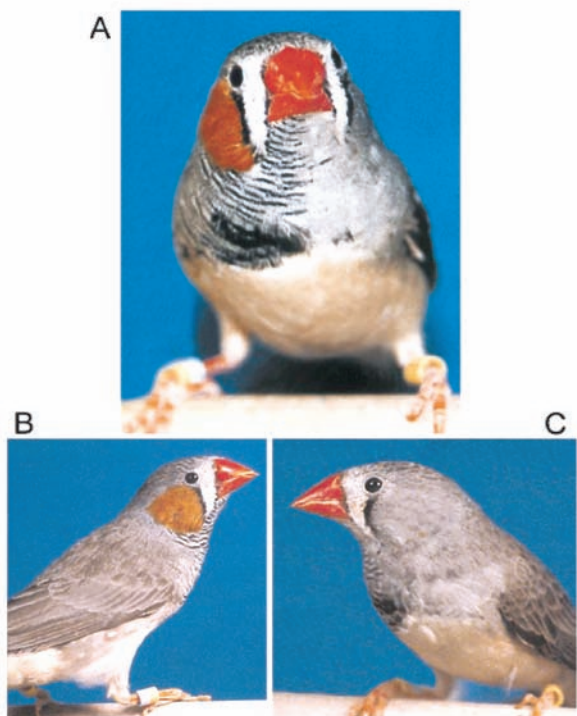


Fig. 13.3 A gynandromorphic zebra finch, (A). This bird showed male plumage on the right side (B), and female plumage on the left side (C). Reproduced with permission from Agate *et al.* 2003. Proceedings of the National Academy of Sciences USA, 100, 4873-4878, Fig. 1. Copyright (2003) National Academy of Sciences, U.S.A.

The most useful information on the mechanism of avian sex determination has come from the studies of Thorne, Sheldon and their colleagues on a line of triploid ZZW chickens (3A:ZZW). (Thorne and Sheldon 1993). Studies on these birds support the Z-dosage hypothesis, antagonised by a feminising W chromosome that is not dominant. Birds with a ZZW genotype develop as intersexes. At hatching, they have right testes and transient left ovotestes (both testicular and ovarian tissue). They are phenotypically female, but the ovarian component of the left ovotestis regresses during maturation. They become males at sexual maturity, with effectively bilateral testes (Lin *et al.* 1995). The transient ovarian development of these triploid chickens, despite the presence of two Z chromosomes, suggests that the W chromosome does carry an ovary-determining gene. However, it can be antagonised by Z-linked (male) gene/s, because the ovarian tissue seen in the triploid birds is not maintained. At present, then, neither the Z dosage nor the dominant W hypotheses for avian sex determination can be categorically excluded.

13.4 GONADAL SEX DIFFERENTIATION IN BIRDS

Our understanding of sex determination and gonadal differentiation in birds comes almost entirely from studies on the chicken embryo (*Gallus gallus domesticus*). In the chicken, the embryonic gonads develop as thickenings of the coelomic epithelium on the ventromedial surface of the mesonephric (embryonic) kidneys (Fig. 13.4A). The undifferentiated or “bipotential” gonads are apparent by day 3.5 of incubation. (Total incubation time is 21 days.) This corresponds to developmental stage 21, according to the staging scheme of Hamburger and Hamilton (HH) (1951). At this early stage, the gonads appear morphologically identical in both sexes. They comprise an outer epithelial layer of somatic cells (the cortex), and an underlying medulla of loose epithelial cords interspersed with mesenchymal cells (Fig. 13.4B). The medullary cords are thought to derive from the proliferation and ingrowth of the overlying epithelial (cortical) layer (Merchant-Larios *et al.* 1984; Rodemer-Lenz 1989). These cells are critical to gonadal development, because they go on to form the seminiferous tubules in male embryos, and are the site of estrogen synthesis in female embryos. The primordial germ cells (PGCs) originate in the epiblast, and migrate through the bloodstream to the bipotential gonads, where they settle primarily in the gonadal cortex in both sexes (Meyer 1964; Fujimoto, *et al.* 1976; Kuwana 1993; Petitte *et al.* 1997). There is an early asymmetry in the embryonic chicken gonad with respect to germ cell distribution, with more PGCs colonising the left gonad (Zaccanti *et al.* 1990). Gonadal sex differentiation can occur in both sexes in the absence of PGCs, as assessed by histology and hormonal output (McCarrey and Abbott 1978, 1982). Testis versus ovary development is therefore dependent upon the somatic tissues (cortex and/or medullary cells). Interestingly, studies on experimentally-induced ZZ/ZW chimeric chicken embryos indicate that genetically male (ZZ) gametes can develop into ova in a ZW (female) gonad, while genetically female (ZW) gametes can develop into spermatocytes in a male gonad (Kagami *et al.* 1995; Abinawanto *et al.* 1998; Naito *et al.* 1999). These observations contrast with the situation in mammals, in which genetically female (XX) germ cells fail to enter spermatogenesis if re-located into male gonads, due in part to the requirement of a Y chromosome. This requirement is due to the fact that the Y sex chromosome carries genes necessary for spermatogenesis. However, the studies of chimeric chicken embryos would indicate that all genes required for both oogenesis and spermatogenesis in birds are not sex-linked, but autosomal.

In the chicken embryo, the onset of morphological differentiation of the gonads into testes or ovaries occurs between day 5.5 and 6.5 (HH stages 28–30) (Fig. 13.4A) (Romanoff 1960; Stahl and Carlon 1973; Ebensperger *et al.* 1988). In ZZ embryos, the disorganised medullary cords thicken and become organised into patent testis (seminiferous) cords (Fig. 13.4B). The organization of these cords is due to the differentiation of Sertoli cells. As in mammals, this process appears to be the key cellular event in the initiation of testis formation.

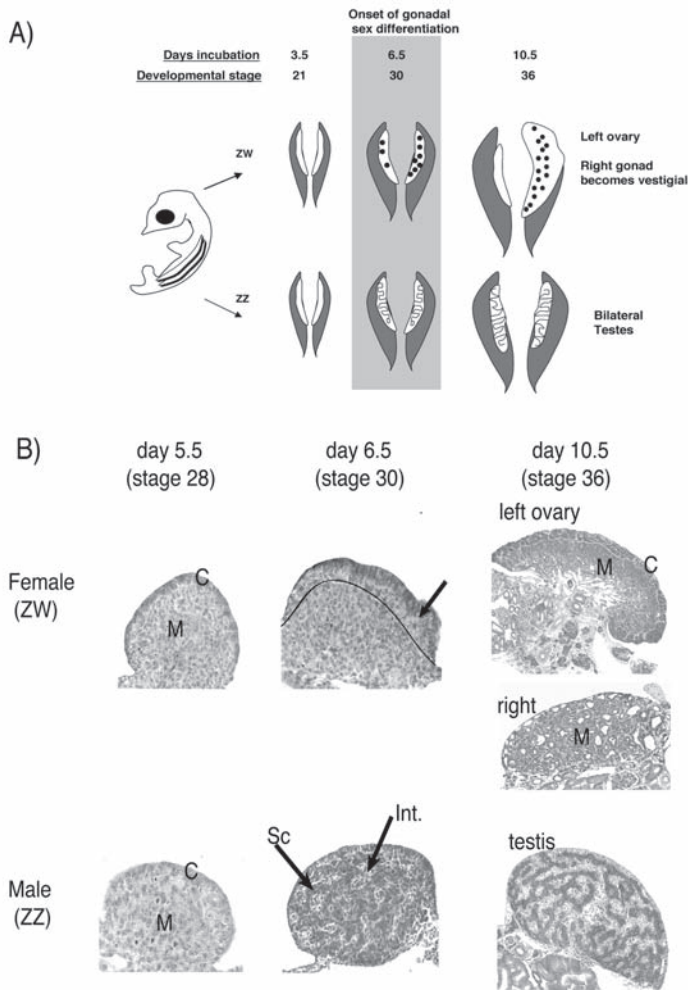


Fig. 13.4 Gonadal sex differentiation in the chicken embryo. **A.** Schematic of differentiation from day 3.5 (undifferentiated), through day 5.5-6.5 (morphological differentiation begins), to day 10.5 (differentiation essentially complete). Gonads are shown in white, mesonephric kidneys shown in grey, germ cells shown in black. **B.** Histology of embryonic gonads. At day 5.5 (stage 28), gonads are histologically undifferentiated, with an outer cortex (C) and underlying medulla (M). At day 6.5 (stage 29-30), ZW gonads have a thickened cortex (defined here with a black line), with proliferating primordial germ cells (arrow). Medulla remains unorganized. In ZZ gonads, seminiferous cord organization (Sc), become distinct from surrounding interstitium (Int.). By day 10.5 (stage 36), the left ZW gonad is an ovary, with thickened cortex (C) and fragmented medulla (M). The right gonad has a fragmented medulla but no cortex. The testis in ZZ embryos is well developed. Original.

The outer cortical zone becomes reduced to a monolayer of epithelium in males. Meanwhile, in ZW (female) embryos, gonadal sex differentiation is asymmetric. Initially, cells of the cortex proliferate (Fig. 13.4B) in both left and right gonads (see also Volume 6A, Chapter 4). This is first obvious at day 6.5 in the chicken embryo. Shortly thereafter, the medullary cords become fragmented and vacuolated, forming so-called lacunae. However, the cortex subsequently regresses in the right gonad (from day 7.5), leaving a small gonad with only a well-developed medulla. This right gonad is non-functional in the adult chicken. In contrast, the left gonad develops into an ovary proper, with meiotic germ cells distributed throughout the well-developed outer cortical layer (Fig. 13.4B). By day 10.5 (HH stage 36), the asymmetry of female gonadal development is very obvious, while bilateral testis development is apparent in males (Fig. 13.4A and B). (The left testis is slightly larger than the right in males, but the male urogenital system does not show the extreme asymmetry seen in females).

The degree of regression seen in the right gonad varies among bird species. Some raptors (hawks, falcons) have bilateral ovaries, others have very small right gonads, while the right gonad is apparently absent altogether in owls (reviewed in Romanoff, 1960). The molecular mechanism underlying gonadal asymmetry in female embryos is unclear, but genes such as estrogen receptor alpha and bone morphogenetic protein-7 are down-regulated in the regressing right gonad (Andrews *et al.* 1997; Hoshino *et al.* 2005). In the left gonad of female embryos, there is a rapid proliferation of germ cells prior to their entry into meiotic prophase. This is then followed by folliculogenesis (see Volume 6A, Chapters 4 and 6). Presumptive granulosa cells encircle meiotic germ cells, and loose thecal cells appear. The granulosa cells are thought to be homologous to the Sertoli cells of males (with the same epithelial origin in the cortex or medulla, and with a similar germ cell nurturing function), while the origin of the thecal (endocrine) cells is less clear.

As in mammals, the embryonic (mesonephric) kidneys contribute cells to the developing testes of avian embryos (Rodemer *et al.* 1986; Rodemer-Lenz 1989). *In vitro* experiments using embryonic chicken gonads cultured together with embryonic quail gonads show that mesenchymal cells migrate from the quail mesonephros specifically into the male chicken gonad at the time of gonadal sex differentiation. This process does not occur in females over the same time frame (Smith *et al.* 2005). The immigrating cells contribute to the so-called interstitial cell population (Fig. 13.4B), that is, those cells that are distributed around the developing seminiferous cords. Interstitial cells give rise to at least three different cell types: the testosterone-producing fetal Leydig cells, peritubular myoid cells with muscle-cell type features, and vascular endothelial (blood) cells. It is unclear which of these interstitial cell types derive from the immigrating mesonephric cells, but it includes vascular cell precursors. The cell migration process has been shown to involve a conserved platelet-derived growth factor (PDGF) signalling pathway (Smith *et al.* 2005).

In birds, as in eutherian mammals, differentiated testes and ovaries then induce downstream aspects of sexual phenotype (Fig. 13.1). So-called secondary sexual differentiation is largely mediated by the release of gonadal sex steroid hormones, namely, estrogen and testosterone. In males, testosterone usually controls the formation of features such as spurs and wattles. However, some male traits depend upon the absence of estrogens. These traits are “default” or neutral in males. For example, the external genitalia (genital tubercle) and syrinx (vocal organ) develop in the male mode unless estrogen is present to block such development, as in normal females (reviewed in Romanoff 1964). Similarly, in many cases the bright male plumage is a “default” state, being actively inhibited by estrogen in females. Loss of testosterone through castration in male peacocks has no effect on their gaudy plumage, whereas castration of females, and hence a loss of estrogen, induces the male-type plumage (reviewed in Owens and Short 1995). This is an interesting contrast to mammals, in which female is the neutral state for many sexually dimorphic characteristics, such as external genitalia, and the male state is induced by testosterone. In addition, estrogen has a central role in the embryonic differentiation of the ovary itself in birds, unlike in mammals (see section 13.4 below). Recent studies on gynandromorphic birds (male on one side and female on the other), indicate that some sexually dimorphic characteristics such as the brain neural song circuit may be partly controlled by direct genetic mechanisms (Agate *et al.* 2003). Therefore, in birds, sex-determining genes may be acting directly in different tissues rather than tissues responding to hormonal stimuli from the gonads alone.

13.5 GONADAL HORMONES AND AVIAN SEX DETERMINATION

Hormones play an important role in avian gonadal differentiation. It was shown many years ago that sex reversal can be induced in avian embryos by injecting estrogenic compounds into eggs, or by disrupting estrogen function (reviewed in Romanoff 1964, and in Scheib 1983). Specifically, inhibition of the estradiol-synthesising enzyme, P450 aromatase, can induce testis formation and a permanent male phenotype in chickens (Elbrecht and Smith 1992; Vaillant *et al.* 2001). This led to the discovery that aromatase plays a key early role in gonadal (ovarian) sex differentiation. Aromatase catalyses the synthesis of estrogen from androgen. The aromatase gene is expressed only in female gonads (both left and right) at the onset of sexual differentiation (between day 6.0–6.5; stages 29–30). (Smith *et al.* 1997; Nakabayashi *et al.* 1998; Nishikimi *et al.* 2000). Aromatase enzyme is strongly expressed in the medullary cells of female gonads (Fig. 13.5A). In female embryos treated with a single dose of the aromatase inhibitor, fadrozole, at day 3.5, the left gonad fails to form a normal ovary, while the right gonad becomes a testis. In these organs, aromatase expression is virtually abolished (Fig. 13.5B). Another enzyme involved in estradiol synthesis, 17- β -hydroxysteroid dehydrogenase

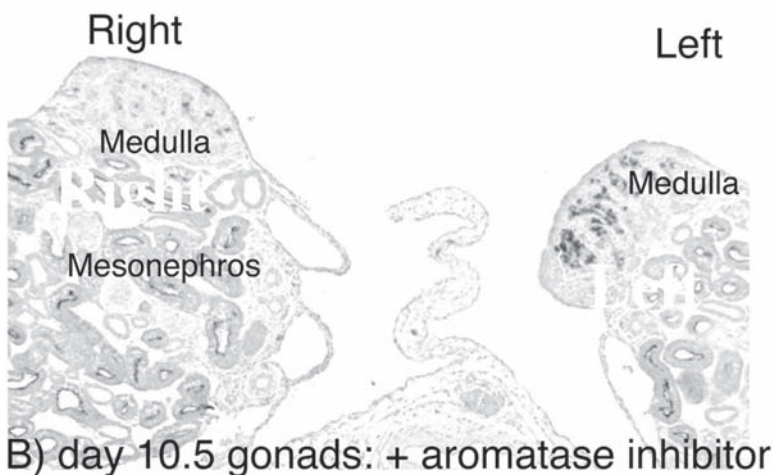
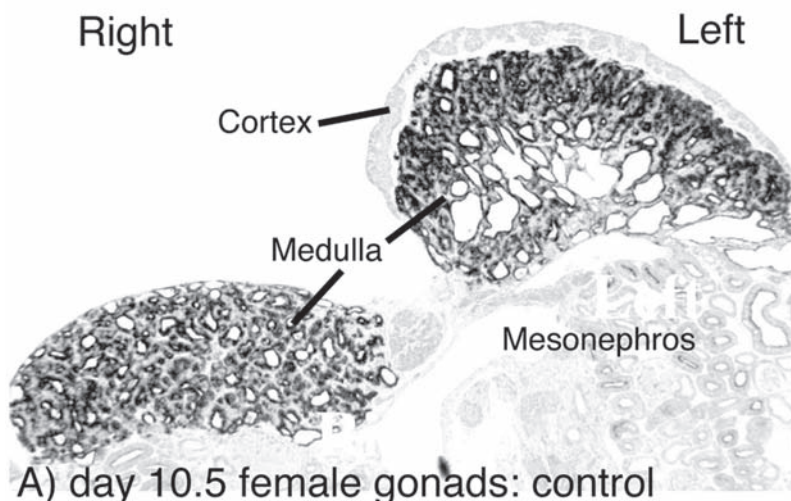


Fig. 13.5 Immunohistochemical localization of aromatase protein in the control ZW embryos and those treated with aromatase-inhibitor (AI) (day 10.5). In control females (ZW), both left and right gonads show strong aromatase enzyme in the medulla (black staining). In embryos treated with AI at day 3.5, the left gonad had residual aromatase, and is small and masculinised (no cortex develops). The right gonad completely lacks aromatase enzyme and is testicular (seminiferous cords in medulla, no cortex). The AI, fadrozole, blocks activity of the aromatase enzyme, preventing estrogen production, but it must also block aromatase synthesis, as shown above. This is presumably mediated by the blockage of estrogen, preventing positive feedback regulation of the *aromatase* gene. Original.

(17- β HSD), is also only expressed in female gonads from day 6.5. Other upstream enzymes within the steroid hormone synthetic pathway are expressed in both sexes from earlier stages. Therefore, the ability to make estrogen is restricted to females (ZW embryos) at the time of gonadal differentiation, and is indeed required for ovarian development. It is likely that a master female determining gene activates both aromatase and 17- β HSD as an early step in ovary formation. In contrast to the central role of estrogen in ovary formation, testosterone does not appear to be required for testis formation in male birds.

The right rudimentary gonad of female chickens has masculine potential. If the left ovary is lost due to disease or castration, the right gonad can develop into a testis. It is thought that this is due to a loss of estrogen from the left ovary. However, if so, the effect may be indirect because the right gonad does not form a testis in birds that are both castrated and hypohesectomised (gonads and pituitary gland ablated; reviewed in Kagami and Hanada 1997). It is noteworthy that naturally occurring male-to-female sex reversal has never been observed, in contrast to the female-to-male sex reversal that can occur due to a diseased left ovary. This suggests that the W chromosome may indeed be a prerequisite for female development. Genetically male (ZZ) embryos treated with exogenous estrogens can be feminized, forming ovotestes, but the effect is transient. The susceptibility of male embryos to estrogens can be explained by the fact that both sexes express estrogen receptor alpha in the gonadal cortex during development. In males, this expression is temporary (Andrews *et al.* 1997; Nakabayashi *et al.* 1998).

Experimentally, female-to-male sex reversal can also be achieved by grafting embryonic testes onto the extraembryonic coelom of ZW (genetic female) embryos prior to sexual differentiation (Rashedi *et al.* 1983; Maraude *et al.* 1990). Interestingly, both left and right ZW gonads develop as testes (in contrast to aromatase inhibition in ZW embryos, which induces a right testis but only partial masculinizes of the left gonad). It is thought that the masculinizing effect of differentiated testes is due to the release of Anti-Müllerian Hormone (AMH) from the graft. In mammals, AMH is produced by Sertoli cells soon after their differentiation in male embryos. It triggers the regression of the paired Müllerian ducts in males, which otherwise differentiate into Fallopian tubes, uterus and upper vagina. In chicken embryos, the AMH gene is expressed in both sexes, mediating regression of both ducts in males, as in mammals, but also inducing regression of the right duct in females (see Volume 6A, Chapter 4). The remaining left duct in females forms the oviduct. However, AMH is more strongly expressed in male embryos compared to females from just prior to gonadal sex differentiation (stage 25-27) (see Fig. 13.6) (Oréal *et al.* 1998; Smith *et al.* 1999a). While AMH lies downstream in the sex-determining pathway in mammals, in birds it may have a more central role in gonadal differentiation, as suggested by its early sexually dimorphic expression pattern, and the testis graft experiments. The promoter region of the chicken *AMH* gene harbours potential estrogen

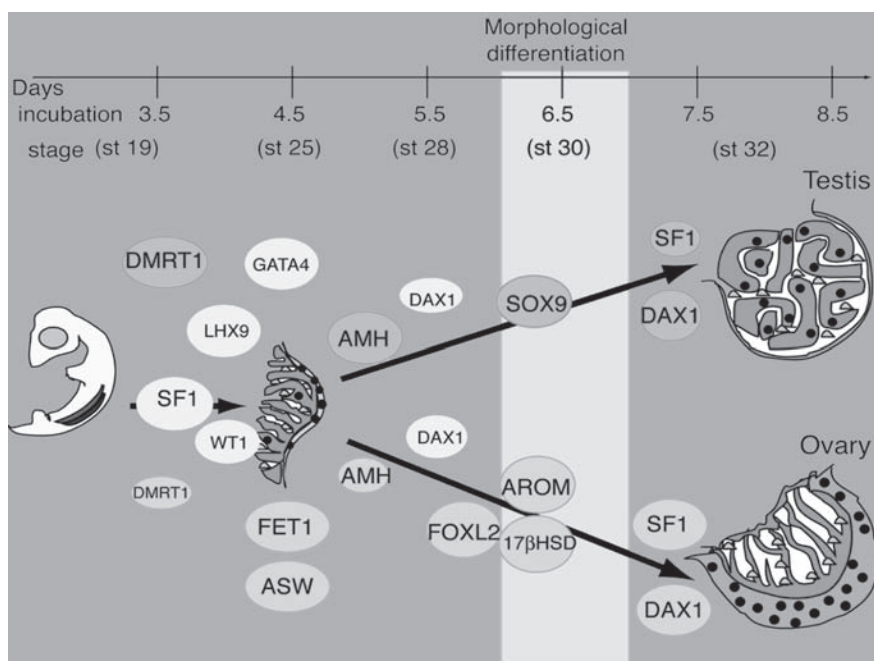


Fig. 13.6 Gene expression during gonadal sex differentiation in the chicken embryo. Circles denote the onset of gene expression. Circle size represents relative expression level compared to the opposite sex. Yellow circles denote genes expressed at similar levels in both sexes, blue circles denote male up-regulated genes, pink circles denote female up-regulated genes. The gonad is morphologically undifferentiated until stage 29-30 (Pale box). Modified from Smith and Sinclair (2004). *Bioessays*, 26: 120-132, Fig. 4.

response elements (Oréal *et al.* 1998), indicating that the gene could be regulated by estrogen. Thus, in females, AMH expression may be kept in check by estrogen, synthesised by aromatase from day 6.5 (stage 30), while the absence of estrogen production in males may allow strong up-regulation of AMH and testis formation. Conversely, AMH might negatively regulate aromatase, as can occur in mammals (Vigier *et al.* 1989). Under this scenario, AMH and aromatase would operate as functional antagonists in avian sex determination. Other potential binding sites in the cAMH promoter include SOX and Steroidogenic Factor-1 (SF1) sites. The SOX and SF1 genes are implicated in gonadal differentiation in birds (see below, and Fig. 13.6).

13.6 CONSERVED GENES IN AVIAN SEX DETERMINATION

While the basic mechanism of avian sex determination is currently unknown, a number of genes have been identified which are expressed in the gonads and are presumed to play a role in gonadal differentiation. The following discussion summarizes our understanding of these genes in avian gonadal

development, based almost entirely on studies in the chicken embryo. A common feature of genes described in this section is that they are shared between mammals and birds, and are thought to be part of the ancestral sex-determining pathway. However, in some cases, genes appear to have been recruited to different positions in the pathway in the two vertebrate groups.

13.6.1 Genes Expressed during Early Gonadal Development

During formation of the undifferentiated gonad, genes encoding transcription factors are expressed. These include the orphan nuclear receptor, Steroidogenic Factor-1 (*SF1*), the Wilm's Tumour associated gene (*WT1*) and a LIM homoeobox gene, *LHX9* (Kent *et al.* 1995; Smith *et al.* 1999a, 1999b, 2000; Oréal *et al.* 2002). The signaling molecule *Wnt4* is also expressed in the early chicken gonad (Oréal *et al.* 2002). All of these are expressed at similar levels in both sexes (Fig. 13.6). Targeted mutagenesis of these genes in mice causes failure of proper gonadal development, and it is likely that these genes also play a role in the formation of the early gonadal primordium in birds.

The onset of gonadal sex differentiation in the chicken embryo coincides with the expression of aromatase and 17- β HSD enzymes in the medulla of female gonads (between stages 29-30; days 6.0-6.5) (Fig. 13.6). The factor responsible for activation of these enzymes is not known, but it must directly or indirectly involve a female-determining gene. One factor that may participate in aromatase activation is Steroidogenic Factor-1 (*SF1*). In addition to its requirement for early gonad formation, *SF1* in mammals is an important regulator of the sex steroid synthetic pathway. It has been shown to regulate most steroidogenic enzyme genes, including aromatase (Lynch *et al.* 1993; reviewed in Parker and Schimmer 1997). At around the onset of gonadal sex differentiation in the chicken embryo, *SF1* gene expression appears higher in female embryos compared to males, at a time when aromatase expression is activated (reviewed in Smith and Sinclair 2004). A potential *SF1*-binding site is present in the chicken aromatase promoter region (C. Smith, unpubl.). Elevated *SF1* in genetic females may therefore play a role in the initiation of aromatase and estrogen synthesis during ovarian differentiation. However, *SF1* is also expressed in genetic male embryos, initially at similar levels to females (Smith *et al.* 1999b), yet aromatase is not activated in males. This implies that other factors are needed for activation of the key aromatase gene in female embryos.

One such factor may be the winged helix transcriptional regulator, *FOXL2* (Forkhead box-transcription factor, class L2). *FOXL2* was first identified in mammals as a gene deleted in Polled intersex goats, which show varying degrees of female-to-male sex reversal (Pailhoux *et al.* 2001). In mouse and human, *Foxl2* deletions disrupt normal ovarian development (Crisponi *et al.* 2001; Schmidt *et al.* 2004). In the chicken, *FOXL2* messenger RNA is expressed in female but not male embryonic gonads from day 5.5 (stage 28) (Löffler *et al.* 2003), just prior to aromatase expression from day 6 (stage 29-30) (Fig. 13.7). Furthermore, *FOXL2* and aromatase expression co-localise in the medullary

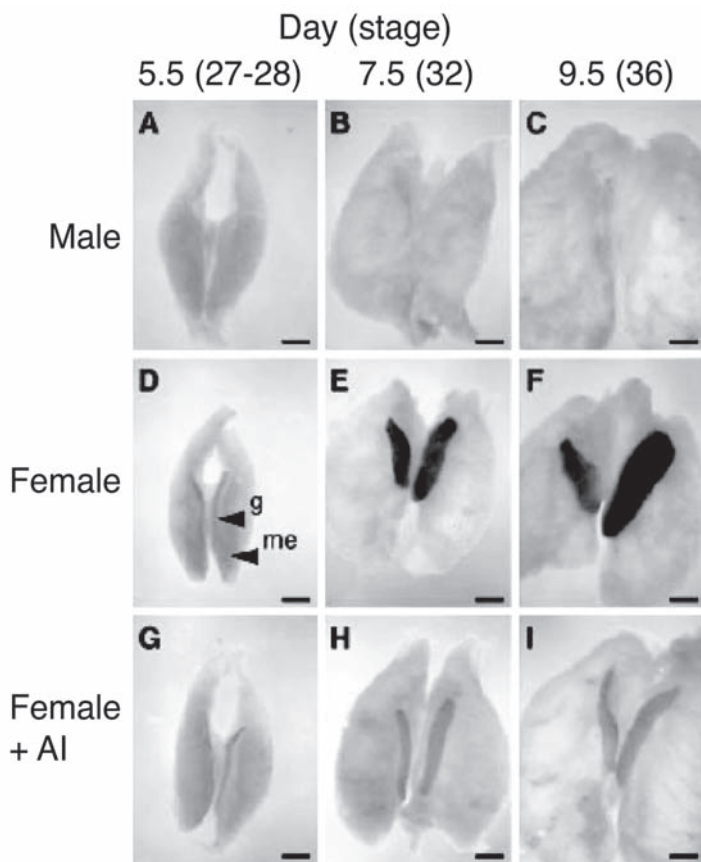


Fig. 13.7 Expression of the forkhead transcription factor, *FOXL2*, during gonadal development and following sex reversal in ZW embryos treated with aromatase inhibitor. Using whole mount in situ hybridisation, mRNA localization is shown by black staining. *FOXL2* is not expressed in ZZ (male) embryonic gonads (**A**, **B**, **C**). In normal females (ZW), *FOXL2* is expressed in the gonads (g) from day 5.5 (stage 27-28), but not in the adjoining mesonephros (me) (**D**, **E**, **F**). In genetic female embryos (ZW) treated with aromatase inhibitor, *FOXL2* expression is significantly reduced, but not abolished (**G**, **H**, **I**). Reproduced with permission from Hudson *et al.* 2005. *Developmental Dynamics*, 233: 1052-1055, Fig. 2.

cords of female embryos, and a potential binding site for *FOXL2* exists in the aromatase promoter region (Govoroun *et al.* 2004; Hudson *et al.* 2005). Genetically female chicken embryos treated with an aromatase inhibitor show reduced but not abolished *FOXL2* mRNA expression (Fig. 13.7), supporting the idea that *FOXL2* lies upstream of aromatase, but that aromatase (estrogen) feedback may normally maintain its expression (Hudson *et al.* 2005). Other factors that may regulate aromatase activity in the early forming ovary include the pituitary gonadotrophin hormones, LH and FSH. LH and FSH receptor

mRNAs are detectable in both sexes from as early as day 4, becoming elevated in female gonads from day 6 (stage 30) (Akazome *et al.* 2002). However, the fact that embryonic chicken and duck gonads can commence sexual differentiation when isolated *in vitro* suggests that pituitary hormones are not initially required (Haffen 1975; Smith *et al.* 2005).

Another potential role for SF1 in developing avian gonads is the up-regulation of AMH. Just prior to aromatase and 17- β HSD activation in female chicken gonads, AMH shows specific up-regulation in males (Fig. 13.6). It has been suggested above that AMH may have an important role in the early stages of gonadal sex differentiation in birds, in contrast to mammals. Up-regulation of this hormone in male embryos may contribute to Sertoli cell differentiation and the organisation of seminiferous cords. A potential SF1 binding site has been noted in the chicken AMH promoter region (Oréal *et al.* 1998), while, in the mouse embryo, SF1 has been definitively shown to contribute to *AMH* gene activation (Shen *et al.* 1994). However, as noted above, *SF-1* expression also occurs in females at day 6.0-6.5, so other factors seem implicated.

13.6.2 *SOX* Genes and Avian Gonadal Development

In mammals, the Y-linked *SRY* gene initiates testis development in males (Sinclair *et al.* 1990; Koopman *et al.* 1991). *SRY* is the defining member of a large family of developmental regulatory genes, all sharing a DNA-binding motif called the *SOX-box* (SRY-like HMG Box). *SOX* genes encode transcription factors, which bind to target genes and regulate their expression. *SRY* is absent in all non-mammalian vertebrates, including birds. However, a number of related autosomal *SOX* genes are expressed, and most of them do not show sexually dimorphic expression (McBride *et al.* 1997; Smith *et al.* 1999a; Takada *et al.* 2005a). The exception is *SOX9*, a male up-regulated gene conserved across vertebrates. In mouse embryos, *Sox9* is necessary and sufficient for testis development (Chaboissier *et al.* 2004; Qin and Bishop 2005). In the chicken embryo, *SOX9* is expressed only in male gonads (medullary cord cells) at the onset of testicular differentiation (between days 6.0 and 6.5) (Fig. 13.6) (Kent *et al.* 1996; Smith *et al.* 2005). This male-specific expression pattern is conserved in quail and duck embryos (Takada *et al.* 2005b). Taken together, these observations indicate that *SOX9* has a role in avian testis differentiation, as in mammals. The mammalian studies suggest that *Sox9* controls Sertoli cell differentiation and/or the organization of these cells into seminiferous cords. In mammals, *Sox9* expression precedes *Amh* expression, and it has been shown that *SOX9* functions together with SF1 and WT1 to regulate the *AMH* gene. However, in the chicken embryo, *AMH* expression begins prior to *Sox9* expression (Fig. 13.6) (Oréal *et al.* 1998; Takada *et al.* 2005a). This indicates that *SOX9* does not activate *AMH* in birds, although it could up-regulate it. Other closely related *SOX* genes, such as *SOX8* and *SOX10*, do not show sexually dimorphic expression in embryonic chicken gonads, as required if they were to activate the *AMH* gene (Takada *et al.* 2005a; Bell *et al.* 2000). The

trigger for *SOX9* activation in birds is not known, although in mammals it is speculated to be *SRY*. In the absence of *SRY*, an alternative mechanism must exist for *SOX9* activation in avians.

13.7 CANDIDATE SEX-DETERMINING GENES IN BIRDS

None of the genes described above are sex-linked in birds. Genes such as *Aromatase*, *FOXL2*, *AMH* and *SOX9* must all lie downstream within the sex-determining pathway in birds. The master sex determinants must reside on the Z and/or W sex chromosomes. The following section considers the two candidate avian sex-determining genes currently under study.

13.7.1 The *DMRT1* Gene and Z Chromosome Dosage

According to the Z dosage hypothesis for avian sex determination, the higher dose of a Z-linked gene in ZZ embryos would trigger testis development, while one dose would result in ovary development. For this hypothesis to apply based purely on gene dosage, Z chromosome inactivation must not occur, or be restricted. In mammals, dosage equalisation of X-linked genes occurs through the global inactivation of most genes on one X chromosome in females. (It is considered that twice the dose of X-linked genes would otherwise be lethal in female embryos.) RT-PCR analysis suggests that dosage compensation also occurs in birds, with males and females showing similar mRNA levels for several Z-linked genes (McQueen *et al.* 2001). However, *in situ* hybridisation of mRNA transcription from the chromosomes indicates that these genes are transcribed from both Z chromosomes in males (Kuroda *et al.* 2001). Taken together, these data indicate that if dosage compensation occurs in birds, it may operate through a mechanism different from that in mammals (that is, not through global inactivation of one sex chromosome in the homogametic sex). One Z-linked gene that appears to escape dosage compensation is the candidate sex determinant, *DMRT1* (*Drosophila* Doublesex and *C. elegans* Mab-3 -Related Transcription factor, #1) (Raymond *et al.* 1998; Nanda *et al.* 1999). *DMRT1* is conserved across vertebrates and is more highly expressed in developing testes compared to ovaries (Smith *et al.* 1999c; Raymond *et al.* 1999). In the chicken embryo, *DMRT1* is expressed in the gonads of both sexes, but is more highly expressed in ZZ (male) embryos, prior to and during gonadal sex differentiation (Smith and Sinclair 2001) (Fig. 13.6). It is of particular interest to note that *DMRT1* is also Z-linked but absent from the large W sex chromosome in the emu, a ratite (Shetty *et al.* 2002). Given that all other Z-linked genes have W homologues in the ancient ratite lineage, the strictly Z-linked occurrence of *DMRT1* in the emu strengthens the possibility that this gene is sex-determining in all birds. However, in the chicken embryo, *DMRT1* expression is higher in ZZ embryos compared to ZW embryos well prior to sexual differentiation (as least as early as day 3.5; (Raymond *et al.* 1999; Smith and Sinclair 2001). Therefore, another gene/s may link early *DMRT1* expression with later expression of male up-regulated genes

such as *AMH* and *SOX9*. Alternatively, *DMRT1* expression may increase from day 3.5 (stage 19) to a threshold at day 6 (stage 29), at which point it activates genes such as *SOX9*. Quantitative RT-PCR shows that the ratio of male:female *DMRT1* expression is particularly high at day 6, more than expected from gene dosage alone (Smith *et al.* 2003). Proof of a role for *DMRT1* in avian sex determination will be demonstrated by transgenic over-expression (McGrew *et al.* 2004) or gene knockdown.

13.7.2 ASW/HINTW: A Candidate Female-determining Gene

In hybridization screens to uncover novel factors involved in chicken sex determination, two independent groups identified a W-linked gene that is highly expressed only in female embryos (Figs. 13.2, 13.6). O'Neill *et al.* (2000) called it ASW (Avian Sex-linked, on the W), without reference to potential function. Hori *et al.* (2000) called it WPKCI (W-linked Protein Kinase C Inhibitor-related). The gene is also called HINTW, because it in fact encodes a derived form of a *Histidine triad nucleotide hydrolase* enzyme (Pace and Brenner 2003). HINT proteins are found throughout eukaryotes and, in mammals, they are autosomally located. The ASW gene is very unusual because it encodes a predicted protein that lacks the key catalytic domain used to define the HINT enzymes (the so-called HIT domain). A bona fide HINT gene is located on the avian Z sex chromosome (HINTZ) (Hori *et al.* 2000), and is presumably the ancestral gene from which ASW has evolved during evolution of the W sex chromosome. The function of the bona fide HINT orthologue, HINTZ, is to hydrolyse nucleotides (AMP or GMP) from lysine residues of proteins (Pace and Brenner 2003).

ASW is a female-specific, W-linked gene in all carinate birds that have been examined (O'Neill *et al.* 2000; Hori *et al.* 2000). In chickens and other birds, the gene is amplified at least 40 times across the small non-heterochromatic end of the W chromosome. In contrast, HINTZ is a single copy gene. In ratite birds, Southern blots of genomic DNA show a single band in both sexes (Hori *et al.* 2000). This suggests that ASW is absent in this group, although it is possible that it is present but not amplified in ratites, and is sufficiently similar to HINTZ that just one band is detected in females. In the chicken, ASW is strongly expressed in the gonads and throughout the embryo from early stages of embryogenesis (at least as early as day 3.5) (O'Neill *et al.* 2000). The bona fide Z-linked HINT, HINTZ, is also expressed in gonads and extra-gonadal tissues (of both sexes) but at lower levels than ASW (Hori *et al.* 2000). It is suggested that ASW may operate as a dominant negative factor in avian sex determination (Hori *et al.* 2000; Pace and Brenner 2003). HINT enzymes normally function as homodimers. ASW may therefore heterodimerise with HINTZ, blocking its catalytic action, leading to a block in the testis pathway, or an induction of the ovary pathway (Parks *et al.* 2004) (Fig. 13.8). It has been found that ASW shows adaptive molecular evolution, having undergone strong positive selection, which supports its putative novel function in female birds (Ceplitis and Ellegren 2004). There are a small number of other W-linked

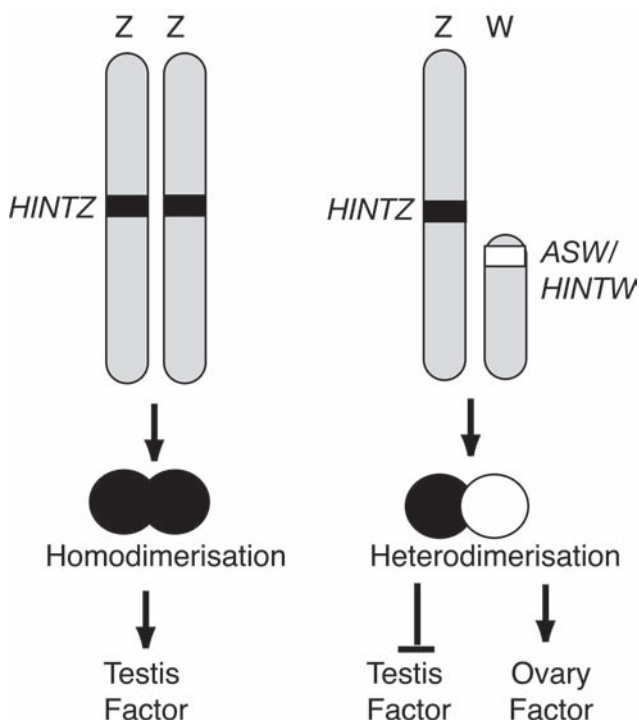


Fig. 13.8 A model for *ASW/HINTW* action in avian sex determination. In ZZ (male) embryos, *HINTZ* forms a functional homodimer, playing a role in male development. In ZW (female) embryos, *ASW* acts as a dominant negative factor, forming a heterodimer with *HINTZ*, interfering with its function, leading to female development. Modified from Smith and Sinclair (2004). *Bioessays*, 26: 120-132, Fig. 5.

genes that are expressed in chicken embryos, such as *CHDW*, *ATP5A1W* and *SPINW* (Ellegren 1996; Fridolfsson *et al.* 1998; Yamada *et al.* 2004). However, these genes have structural and functional orthologues on the Z chromosome. In contrast, *ASW* is clearly differentiated from its Z counterpart, *HINTZ*, and it represents the best current candidate for an ovary-determining gene, at least in carinate in birds.

An avian retroviral sequence, named *FET-1* (Female-Expressed Transcript, #1) has recently been identified on the chicken W sex chromosome (Reed and Sinclair 2003). As expected of a W-linked gene, *FET1* is not expressed in male embryos (Fig. 13.6). However, *FET1* has an asymmetric expression pattern in the gonads of female chicken embryos, being strongly expressed in the left gonad, but down-regulated in the right gonad at the time of sexual differentiation. This is an intriguing expression pattern, given that the only the left gonad differentiates into a functional ovary. *FET1* does not appear to be expressed outside the urogenital system. It is unclear whether the sequence is translated and the potential role of *FET1* in gonadal development, if any, remains to be defined.

13.8 POTENTIAL INTERACTION BETWEEN THE Z AND W CHROMOSOMES IN AVIAN SEX DETERMINATION

A novel model for avian sex determination involves direct interaction between the W and Z sex chromosomes (Fig. 13.9). Teranishi and colleagues identified a 2.2kb tandem repeat sequence on the chicken Z chromosome that is hypermethylated in males (MHM region) (Teranishi *et al.* 2001). Due to this hypermethylation, the MHM region is transcriptionally inactive in the two Z chromosomes of males. However, the region is hypomethylated and transcribed into high molecular weight mRNA from the single Z chromosome of females (Fig. 13.9). The large transcripts do not appear to be translated into protein in females. Instead, the non-coding mRNA coats the female Z near the site of transcription. This could inhibit or reduce transcription of adjacent genes, such as *DMRT1*. Thus, the different methylation patterns between the sexes could set up different gene expression patterns from the Z sex chromosome. Furthermore, the W chromosome is implicated in demethylation and activation of the MHM in the Z chromosome of females. ZZZ (male) triploid chickens show hypermethylation and no transcription from the MHM, while ZZW birds show hypomethylation and transcription from both Z chromosomes. This shows that the presence of a W chromosome, rather than the number of Z chromosomes, induces hypomethylation. Teranishi *et al.* (2001) have therefore suggested that a factor derived from the W chromosome in females may induce demethylation of the Z chromosome, resulting in

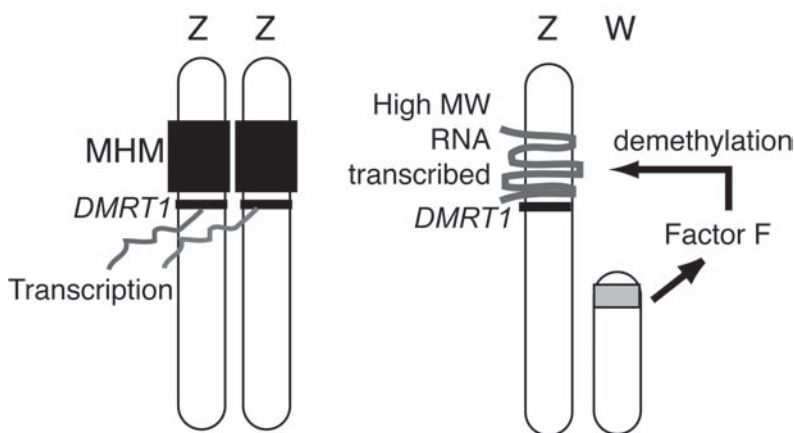


Fig. 13.9 A model for avian sex determination based on differential methylation. In male (ZZ) embryos, each Z sex chromosome has a region that is hypermethylated and transcriptionally silent (MHM). Neighboring genes, such as *DMRT1*, are freely transcribed. In female (ZW) embryos, a W-derived factor induces demethylation of MHM on the Z chromosome. High molecule weight mRNA is then transcribed and coats the Z at the site of transcription, retarding gene activation around this region including the *DMRT1* locus (Teranishi *et al.* 2003). Modified from Smith and Sinclair (2004). Bioessays, 26: 120-132, Fig. 5.

mRNA transcription, which then coats the DNA on the Z and causes reduced or silenced gene expression (Fig. 13.9). This very interesting model could explain the dosage differences between the sexes with respect to *DMRT1*, when other Z-linked genes appear to be subjected to dosage compensation. Sexually dimorphic methylation patterns, triggered by a W-linked gene, may therefore underlie or contribute to avian sex determination. The putative factor from the W is not known, but it may be a demethylase enzyme.

13.9 SUMMARY

The molecular mechanism of avian sex determination is currently unknown, but expression analysis implicates a number of genes within the sex-determining pathway (Fig. 13.6). Much of our understanding of avian sex determination and gonadal sex differentiation comes from studies in the chicken embryo. In this species, the onset of gonadal sex differentiation between days 6 and 6.5 is accompanied by the activation of estrogen synthetic enzymes (aromatase and 17- β HSD) in females, and the *SOX9* gene in males. These genes are likely to be close to the top of the sex-determining cascade in birds. There are currently some good candidate genes that may represent master sex determinants in birds. The Z-linked *DMRT1* gene is expressed more highly in males and may be testis-determining, while *ASW/HINTW* may operate as a female determinant. The differential methylation between the Z and W sex chromosomes may also play an important role in avian sex determination. Current research in this field is focused on the development of transgenic and gene knockdown technologies in birds to clarify the roles of these candidate genes (Smith and Sinclair 2004). It is possible that the master sex-linked genes in birds have yet to be discovered. If so, the search for these genes will be enhanced by the sequencing of the chicken genome.

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